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REVEGETATION AND SOIL DEVELOPMENT ON ANTHROPOGENIC DISTURBANCES IN SHRUB TUNDRA, 50 YEARS FOLLOWING CONSTRUCTION OF THE CANOL No. 1 PIPELINE, N.W.T.

BY

KAREN AMANDA HARPER ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

DEPARTMENT OF GEOGRAPHY

Edmonton, Alberta
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled REVEGETATION AND SOIL DEVELOPMENT ON ANTHROPOGENIC DISTURBANCES IN SHRUB TUNDRA, 50 YEARS FOLLOWING CONSTRUCTION OF THE CANOL No. 1 PIPELINE, N.W.T., submitted by KAREN AMANDA HARPER in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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15 AUGUST, 1994

Abstract

An intensive study of long-term revegetation patterns of Erect Deciduous Shrub Tundra on anthropogenic disturbances was conducted in the summer of 1993 within the CANOL pipeline corridor, Northwest Territories. Soil development, primary and secondary succession were investigated on 10m x 20m sites in vehicle tracks and borrow pits. Data were collected on the cover of all vascular and non-vascular species. Soil temperature, pH, organic matter, moisture and particle size composition were determined. Patterns in plant species composition and soil characteristics among disturbance types were examined using detrended correspondence analysis. The importance of the measured abiotic factors in explaining the differences in species composition was revealed by canonical correspondence analysis.

Significant differences in species composition were evident among disturbance types. Different taxonomic groups exhibited different responses to disturbance. Soil samples in linear disturbances were analogous to those in undisturbed areas. Warmer, drier and less acidic soils in borrow pits contained less organic matter and fine particles than undisturbed soils. Soil temperature was considered the most important measured environmental variable in accounting for the revegetation patterns on disturbances with the microclimate stations. Comparison with a similar study on revegetation in the CANOL corridor in 1978 suggests that revegetation and soil development are proceeding faster on linear disturbances than borrow pits.

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I. INTRODUCTION

Background Literature

In response to the increase in construction and development in the Low Arctic, numerous studies have been focused on the short-term (<10yr) effects of anthropogenic disturbance and revegetation in tundra ecosystems. Several have investigated winter seismic lines (Bliss and Wein 1972; Hernandez 1973; Felix and Raynolds 1989; Felix *et al.* 1992). Others have examined natural recovery of vegetation on disturbances associated with oil spills (Bliss and Wein 1972; Kershaw and Kershaw 1986), roads and vehicle tracks (Kubanis 1980; Chapin and Shaver 1981), borrow pits and gravel pads (Johnson 1987; Bishop and Chapin 1989). Both short- and long-term studies have incorporated numerous disturbances associated with an oil test well (Ebersole 1985), oil and gas exploration (Bliss and Wein 1972; Johnson 1981; McKendrick 1987) and a crude-oil pipeline (Kershaw 1983, 1984).

This research has helped improve construction practices in order to mitigate alterations to tundra plant communities. Investigations have compared the short-term effects of different construction techniques that have been in practice only in recent decades. Results from these studies such as an increase in the dissimilarity between a disturbed and undisturbed shrub tundra community in the first few years following disturbance (Felix *et al.* 1992) emphasize the need for studies on the long-term effects.

Long-term studies have involved the investigation of natural revegetation in tundra communities 10 to 35 years after disturbance (e.g. Johnson 1981; Ebersole and Webber 1983; Komarkova 1983; McKendrick 1987; Densmore 1992). There is still a lack of research on natural revegetation of tundra communities more than 35 years following anthropogenic disturbance. Secondary succession in northern environments is still not complete after several decades as evidenced in changes in species composition even 30-35 years after disturbance (Lawson *et al.* 1978; Kershaw 1984; Ebersole 1985; Kershaw and Kershaw 1987). Ebersole and Webber (1983) expect that the original tundra community will not reestablish on the disturbed site of the Oumalik Test Well for several hundred years. At the Fish Creek Test Well, recovery time was estimated at 600-800 years for mesic upland sites (Komarkova 1983). Webber and Ives (1978) state that complete recovery may be impossible since the present vegetation is a result of past climate. With slow recovery of vegetation in arctic environments, long-term studies are needed to understand primary and secondary succession in tundra plant communities, and to minimize environmental impact from construction in the Low Arctic.

Most of these studies were focused on the effects of disturbance on several different plant communities (e.g.

Komarkova 1983; Kershaw 1984; Ebersole 1987; Felix *et al.* 1992). Although different effects in various plant communities must be recognized, the impact of disturbance type within the same plant community is also relevant to management issues. The type and intensity of disturbance both have important effects on the impact on tundra plant communities (Bliss and Wein 1972; Lawson *et al.* 1978; Ebersole and Webber 1983). Single and multiple passes of vehicles, human trampling, winter and summer vehicle use, bulldozing, roads, bladed trails and borrow pits all have different impacts on vegetation (Ebersole 1985).

Objectives

The abandoned CANOL pipeline corridor provides an excellent opportunity to study the effects of different types of anthropogenic disturbances on the long-term recovery of tundra plant communities. The effects of eight types of disturbance associated with the pipeline on seven different communities was investigated by Kershaw (1983, 1984) in 1977-79. Kershaw surveyed the effects of the pipeline corridor on plant composition, animals and geomorphology above the timberline. Farrington (1988) investigated plant species composition on the road, in borrow pits and on bladed trails and slopes in a subarctic forest community. The Kershaw (1983, 1984) study provides a unique opportunity to investigate ecosystem recovery and successional development from 35 to 48 years following disturbance.

The present study differs from Kershaw's general survey in that it focuses on only one tundra plant community in a smaller area. This narrower focus allows for greater replication and detail in the experimental design, giving more comprehensive and reliable results. Studying the effects within one plant community type should also make it possible to differentiate the effects of disturbance type from other abiotic factors. This intensive investigation of the long-term natural revegetation after different types of disturbance provides further understanding of primary and secondary succession in northern environments, and could provide direction on how to minimize impacts of development in tundra communities.

The primary objective of this study was to determine the long-term effects (48 years following abandonment) of borrow pits and linear (track) disturbances on erect deciduous shrub tundra plant communities. Specific objectives include:

1. Assessment of revegetation on different disturbance types. (Chapter I)
2. Determination of soil characteristics for different disturbance types. (Chapter II)
3. Investigation of the relationship between differences in soil characteristics and plant

species composition 48 years following disturbance. (Chapter III)

An additional objective associated with the first two was:

4. Comparison of plant species composition and soil characteristics between 35 and 48 years following abandonment of the CANOL pipeline.

Description of the Study Site

Field research was conducted from 25 June to 12 August 1993, along the CANOL pipeline corridor east of Macmillan Pass, Northwest Territories (Figure I-1). The study area, located within the Tsichu River Valley Ecosection as identified by Kershaw (1983), extended from Road Mile Post (RMP) 217 to RMP 226 along the western part of the CANOL No.1 East section in the Northwest Territories. The study area was located at approximately 63° north, 130° west and 1300m in elevation.

Topography and parent material varied throughout the study area. Sites west of the base camp were generally located on eskers or alluvial gravel in lower elevations of the valley (Plates I-1, I-2, I-3). A south-west facing slope underlain with glacial till dominated the eastern portion of the study area (Plate I-4). Soils were generally of the Brunisolic order in the western area and the Gleysolic order in the eastern area (for a more detailed description of soils in EDST, see Kershaw 1983a, b).

The CANOL pipeline was constructed during World War II under contract to the U.S. Army to transport crude oil produced at Norman Wells to a refinery at Whitehorse. Finished products were used fuelling military vehicles and aircraft (Kershaw 1983, 1984). The pipeline in the western part of the Northwest Territories section was installed during winter from November 1943 until March 1944 with a minimum 50cm snowpack, and was abandoned in 1945 (Kershaw 1983). The pipeline corridor consisted of a road, and telephone and pipeline rights-of-way (Kershaw 1983, 1984).

Before and during the construction of the CANOL pipeline, no considerations were given to reduce environmental impact, and no rehabilitation efforts were made after abandonment. Some salvage operations were completed in the 1950s (Kershaw 1983, 1984).

Erect deciduous shrub tundra (EDST), the most common plant community type in the study area, dominates the lower elevations within the Tsichu River valley (Kershaw 1983, 1984). EDST was one of seven 'physiognomically-defined' tundra plant communities along the CANOL corridor described by Kershaw (1983). EDST extends across large areas with unbroken cover on imperfectly to well-drained soils over alluvium and till (Kershaw 1983, 1984). Organic soils, Brunisols and Regosols were found in the ecosection where the study site was located; a discontinuous tephra layer was present beneath the organic mat (Kershaw 1983). Permafrost

was either absent or highly localized and well below the surface (Kershaw pers. comm.).

EDST is dominated by tall (>30cm high) shrubs, with an understorey of moss and/or fruticose lichens (Kershaw 1983). All sampling for this study took place exclusively in the *Betula glandulosa - Cladina stellaris* - Moss community, one of the three 'floristically-defined' plant communities in EDST as recognized by Kershaw (1983, 1984). *B. glandulosa* varied from short (50cm) and sparse in the lower elevations in the western half of the study area (Plate I-5), to tall (2m) and dense on the eastern slope of the valley (Plate I-6). The difference in shrub height is due to exposure and mean snow depth (Kershaw 1984). The understorey was a mosaic of fruticose lichens (primarily *Cladina stellaris* and *C. rangiferina*) and pleurocarpic mosses (including *Aulacomnium palustre, Hylocomnium splendens, Polytrichum* spp. and *Sphagnum* spp.), often occurring in the same area (Plates I-7, I-8).

Although most of the CANOL Project disturbance types described by Kershaw (1983, 1984) were found in the study area, only borrow pits, pit access roads, bladed trails and bulldozer tracks were investigated in this study due to re-disturbance of gravel roads and camp yards, and the scarcity of false start roads and oil spills. The disturbances varied in microtopography, compaction, use and grading (Kershaw 1984).

Borrow pits are usually 0.5 to 3m deep with irregular micro-topography and high gravel content. CANOL borrow pits were excavated well below all soil development which would have completely removed all the original vegetation and soil, and any buried seed (Kershaw 1984, pers. comm.). Water is sometimes ponded on the surface; other pits have freer internal drainage (Kershaw 1984; pers. obs.). Vegetation was partially to completely eliminated from pit access roads, and the pre-disturbance soil was either discontinuous, buried or removed. Micro-relief and gravel content were irregular on the loosely compacted mineral access road surface (Kershaw 1983, 1984).

Pipeline and telephone rights-of-way were cleared with a tractor to remove shrubs and level the ground. At least five crews, each with a bulldozer and equipment sled, passed along the pipeline corridor before the pipe was laid directly on the ground. The equipment used for the telephone construction was similar to that for pipeline construction (Kershaw 1983).

Kershaw (1983, 1984) categorizes the linear disturbances used in this study into pit access roads, bladed trails and bulldozer tracks. On bladed trails, the blade of the vehicle was left down which removed vegetation, and often part of the organic soil horizons, to provide a level bed on which to lay the pipe (Kershaw 1983, pers. comm.). As a result, the trails were usually depressed 10-

100cm with slight compaction. Often the conditions of the bladed trails provided a collecting area for water (Kershaw 1984; pers. obs.). In this study, bladed trails were those that were noticeably bladed, indicated by a solid light-toned line on the 1944 aerial photographs (Plate I-9).

In contrast, bulldozer tracks were visible on the aerial photograph as two distinct parallel lines. These tracks were not bladed at all, resulting in no removal of the original soil. Bulldozer tracks often occurred along the telephone right-of-way as indicated by the remains of telephone poles at these sites (pers. obs.). Kershaw (1984) describes bulldozer tracks as two parallel ruts, 5 - 25cm deep with moderate or no compaction of organic horizons.

Two categories of linear disturbances were separated from the 'track' type: 'heavy' use and 'multiple' (or 'multi') tracks. At multiple track sites, several parallel tracks were visible in the area, and could often not be distinguished on the ground (Plate I-4). Heavy use tracks appeared as clearer lines on the aerial photographs, suggesting increased use compared to other tracks. These last two categories always included bulldozer tracks that were not bladed.

Methods

Sites were located in disturbed and undisturbed areas in EDST between RMP 217 and RMP 226 along the CANOL corridor after prior identification on 1944 aerial photographs. A 'site' is defined as a 10m x 20m area within which all sampling occurred. For some linear disturbances narrower than 10m, the shape of the site was altered to 5m x 40m for both the linear disturbance and its associated undisturbed site. A total of 46 sites in the 9-mile (15 km) long study area included 14 pit, 15 linear disturbance and 17 undisturbed sites; of which 6, 4 and 7 were located in the western part of the study area. Sites east of camp on the southwest-facing slope were separated by a few kilometres from sites west of camp in the valley (Figure I-2).

One or two sites were located in all large borrow pits in the study area which had no evidence or likelihood of re-disturbance. 'Pit' site locations were chosen subjectively as representative of the borrow pits. Sites were also located in each pit access road ('access'); these were included in the same category as the linear disturbance sites.

All 'linear' disturbances visible on the 1944 aerial photographs were mapped and numbered every 20m; possible site locations were then selected randomly. Linear disturbance sites that were not discernible in the field were omitted. Others were added to gain a representative set of sites from different areas and linear disturbance types within the study area. These linear disturbances were classified as 'bladed', 'track', 'multi' or 'heavy' based on

examination of the 1944 aerial photographs. Only heavy-use tracks and bulldozer tracks were sampled in the western areas. East of the base camp, all types of linear disturbances were sampled except heavy-use tracks. Linear disturbances were compared only within each area due to regional differences.

'Undisturbed' sites were located in nearby undisturbed EDST with topography similar to the disturbed sites. One undisturbed site was located for each linear disturbance site and for each borrow pit. Disturbance sites without an appropriate undisturbed site were not included.

Two microclimate stations were established to measure soil temperature (Plates I-9, I-10). Each station included two pit sites, two linear disturbance sites and one undisturbed site located in close proximity. All of these sites were located subjectively as representative of each disturbance type. At the east station, the linear disturbance sites included a track and a bladed site. An access and a bladed site were present at the other location. The two pit sites at each location were located at the edge and centre of the pit ('edge' and 'centre' sites).

The second chapter, Plant Community Response is a description of revegetation on the various disturbance types. The focus is on plant species composition, as well as re-establishment of individual species and taxonomic groups. Chapter III, Abiotic Factors, is a discussion of the differences in soil characteristics between undisturbed areas, linear disturbances and borrow pits. Both plant species composition and abiotic factors are integrated in Chapter IV, Integration of Plant Species Composition and Abiotic Factors. The relationships between soil characteristics and plant species composition on the different disturbance types were analyzed using canonical correspondence analysis.

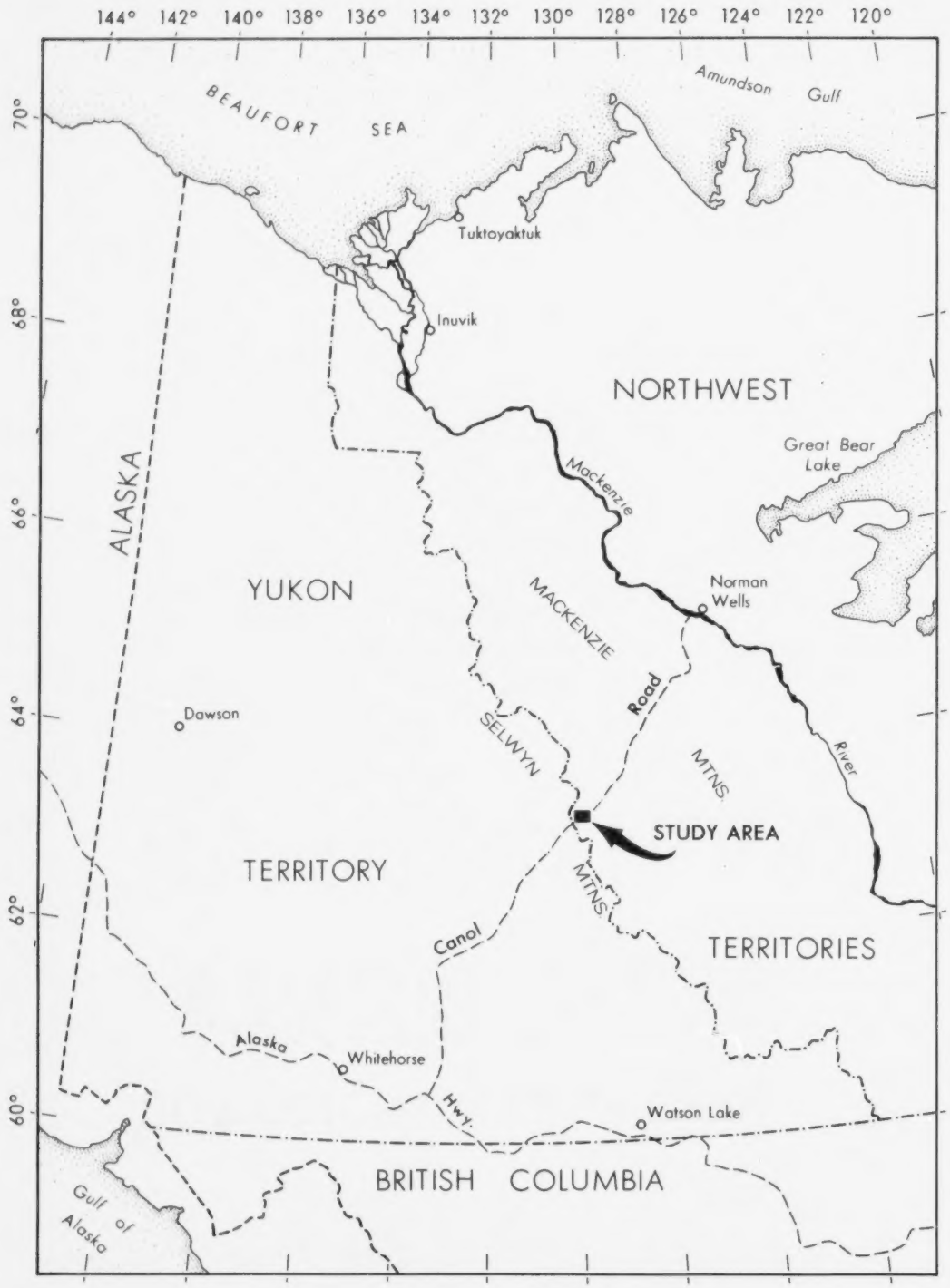

Figure I-1. Map showing location of the study area (Department of Geography, University of Alberta).

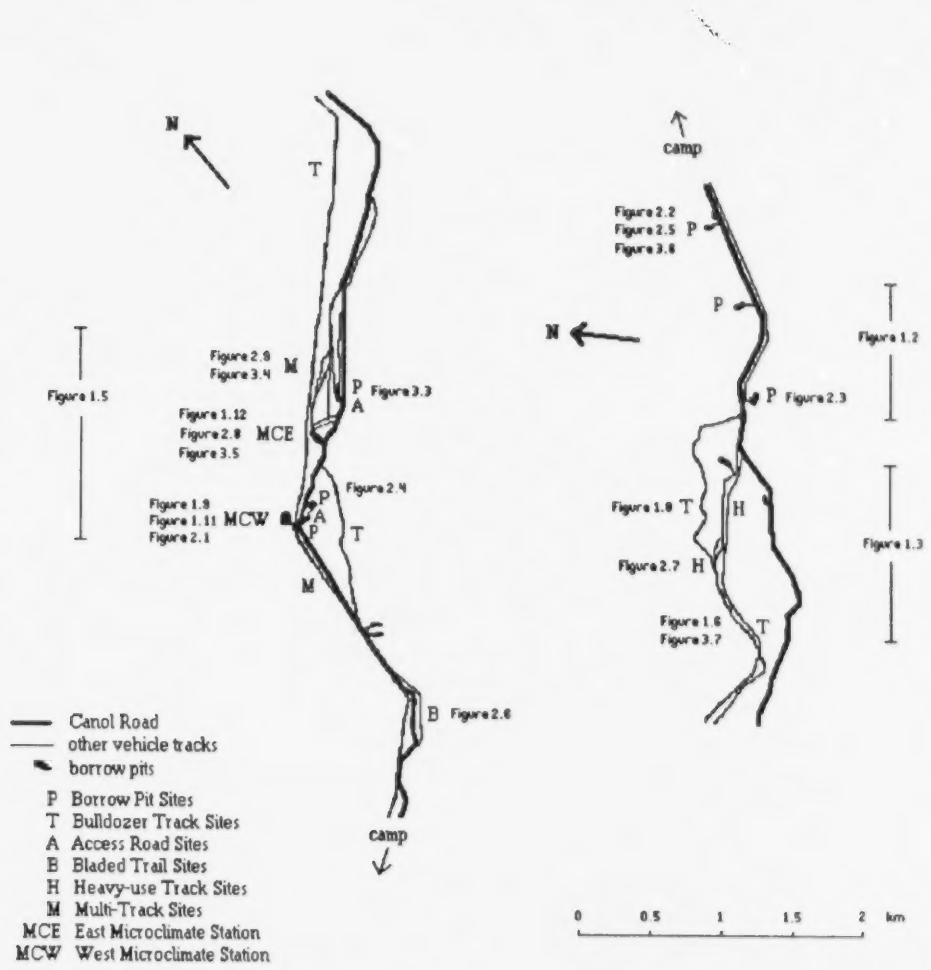

Figure I-2. Map of the study area. Disturbed sites are located with capital letters. The approximate locations of other photographs are indicated. All borrow pits and the most highly visible vehicle tracks, including those not sampled, are shown.

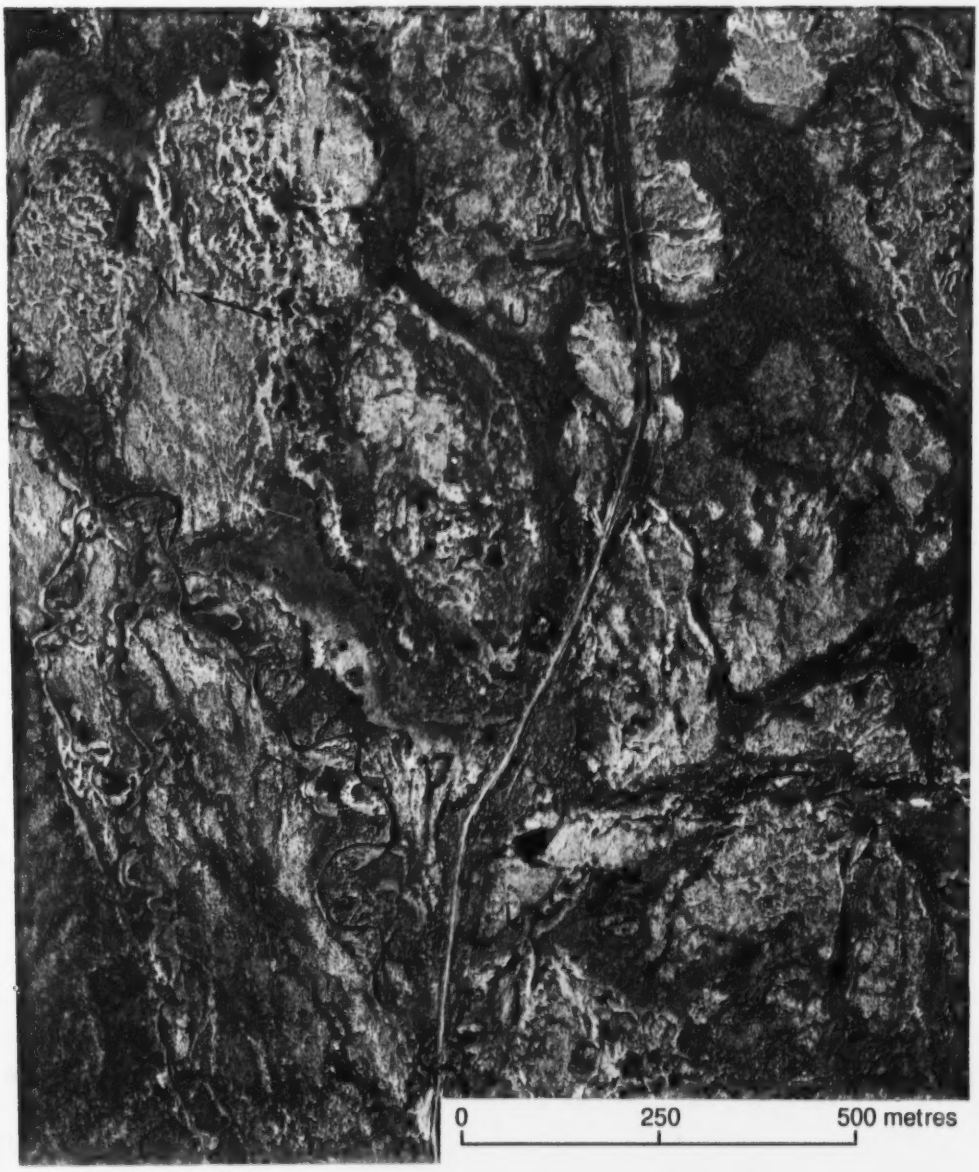

Plate I-1. Aerial photograph (1974) of the western region of the study area. Borrow pits and undisturbed site locations included in the study are indicated by 'P' and 'U'.

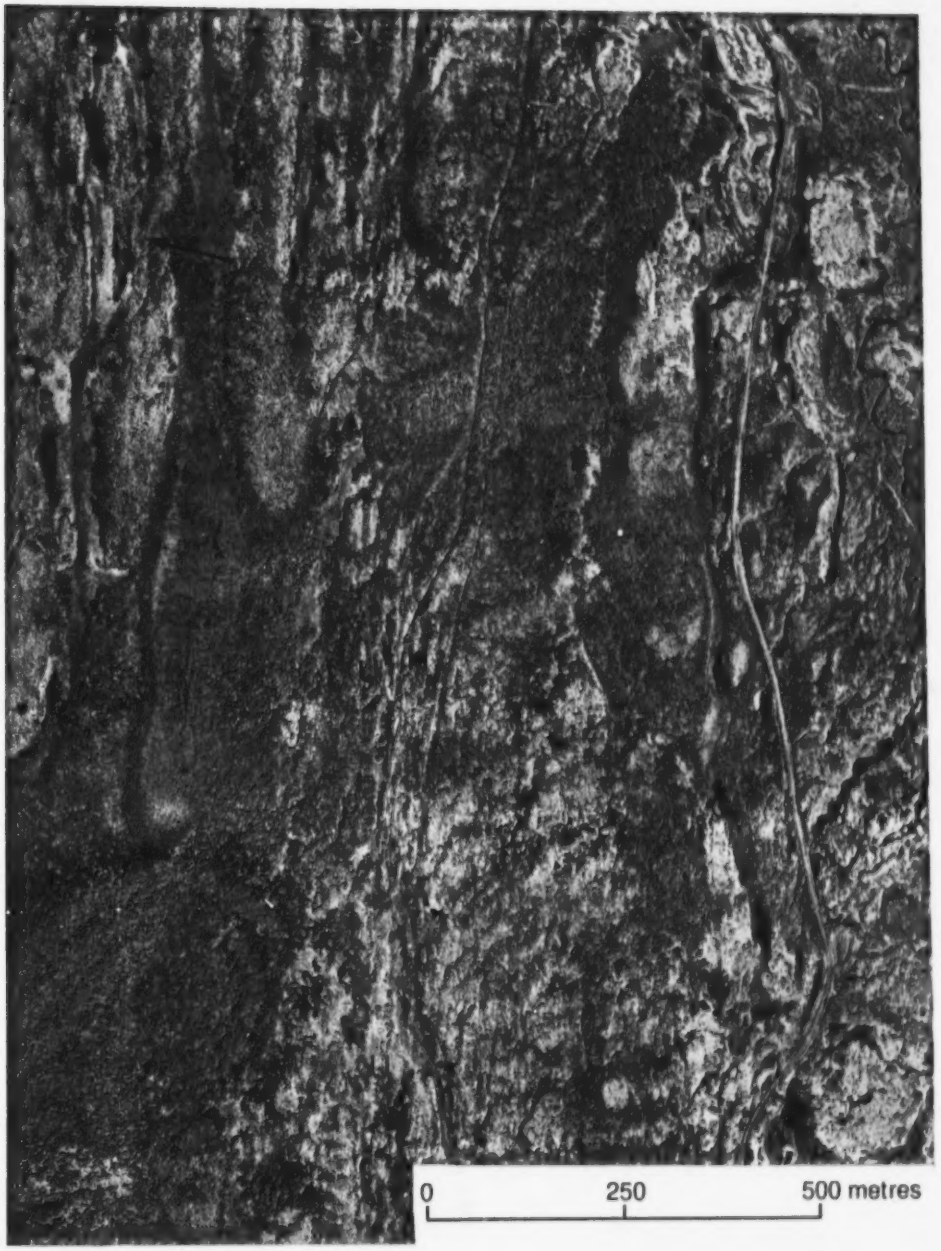

Plate I-2. Aerial photograph (1974) of the western region of the study area. Heavy-use tracks, bulldozer tracks and undisturbed site locations included in the study are indicated by 'H', 'T' and 'U'.

Plate I-3. Photograph taken from an airplane in 1993 of the western region of the study area, looking west.

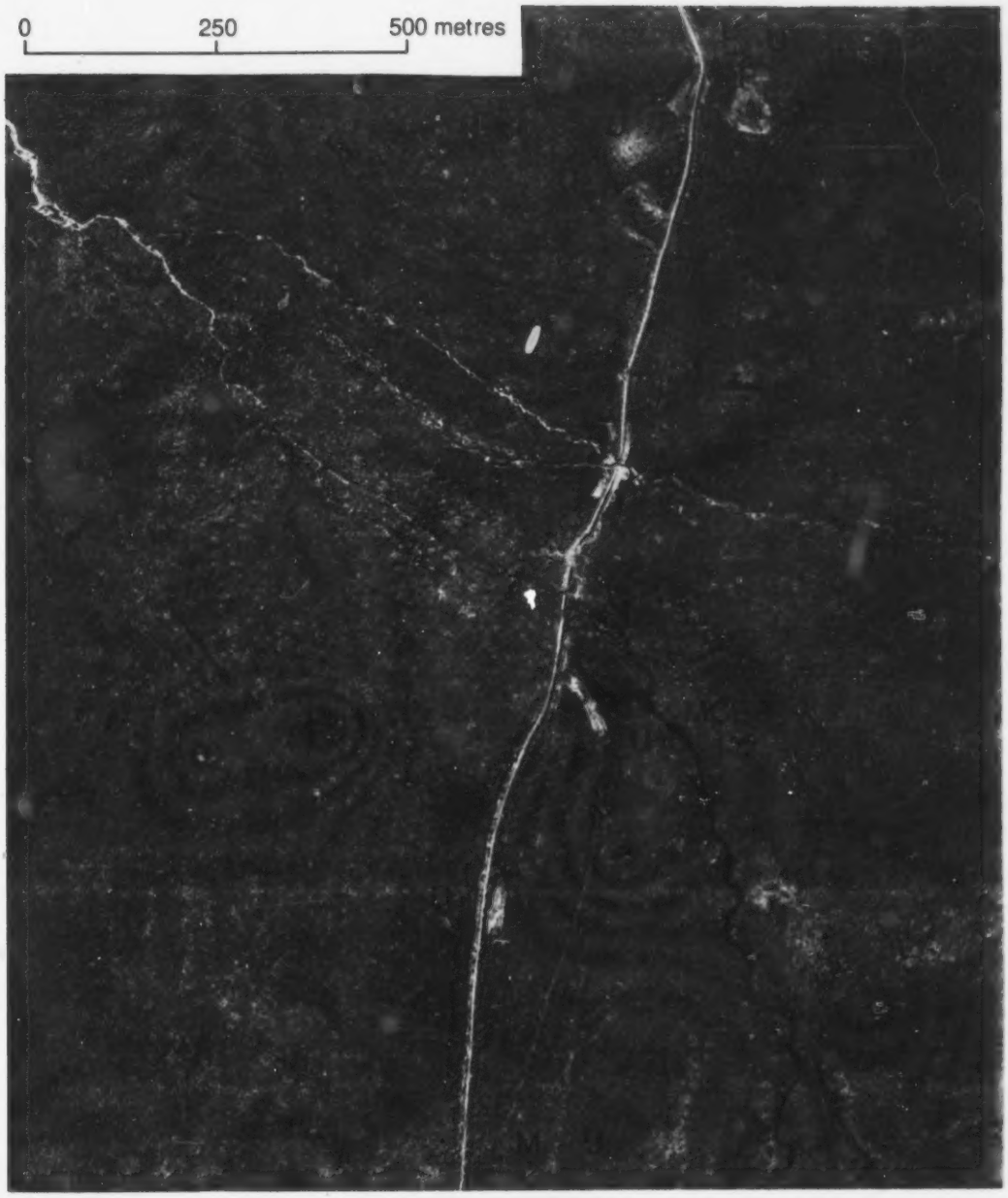

Plate I-4. Aerial photograph (1974) of the eastern region of the study area. Borrow pits, bladed trails, multiple track sites, bulldozer tracks, access roads and undisturbed site locations included in the study are indicated by 'P', 'B', 'M', 'T', 'A' and 'U'. The two microclimate stations are identified by 'MCE' and 'MCW' for the east and west stations.

Plate I-5. Undisturbed shrub tundra in the western region of the study area. Note the sparse cover of *Betula glandulosa* and dense *Cladina* understorey.

Plate I-6. View of the eastern part of the study area in 1993. Note the presence of taller shrubs near the CANOL road. The cover of *Betula glandulosa* is taller and denser than in Plate I-5.

Plate I-7. Understorey in undisturbed shrub tundra in the western region. Note the patches of moss and lichen.

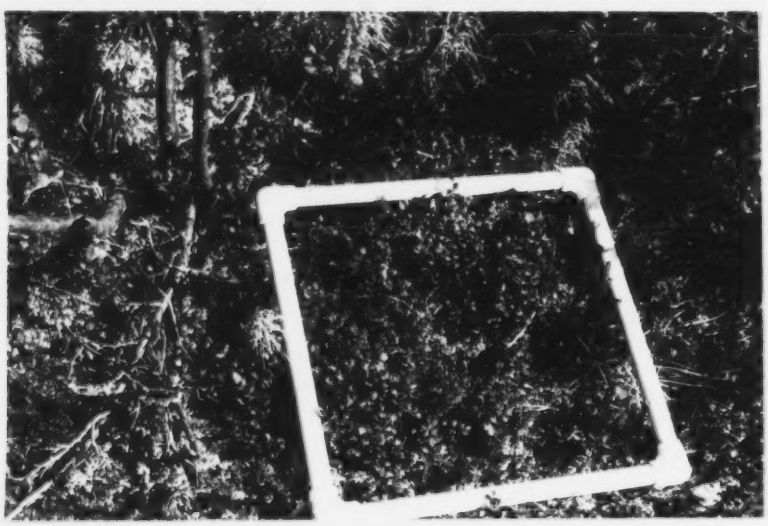

Plate I-8. Understorey in undisturbed shrub tundra in the eastern region. *Empetrum nigrum* and *Vaccinium uliginosum* are visible.

Plate I-9. The western microclimate station on the enlargement of the 1974 aerial photograph. Borrow pits (east and centre), bladed trails, bulldozer tracks, access roads and undisturbed site locations included in the study are indicated by 'P' ('E' and 'C'), 'B', 'T', 'A' and 'U'. Rectangles are not drawn to scale. Note the difference between the solid light-toned line (bladed trail) compared to two distinct lines (bulldozer track), indicated by arrows.

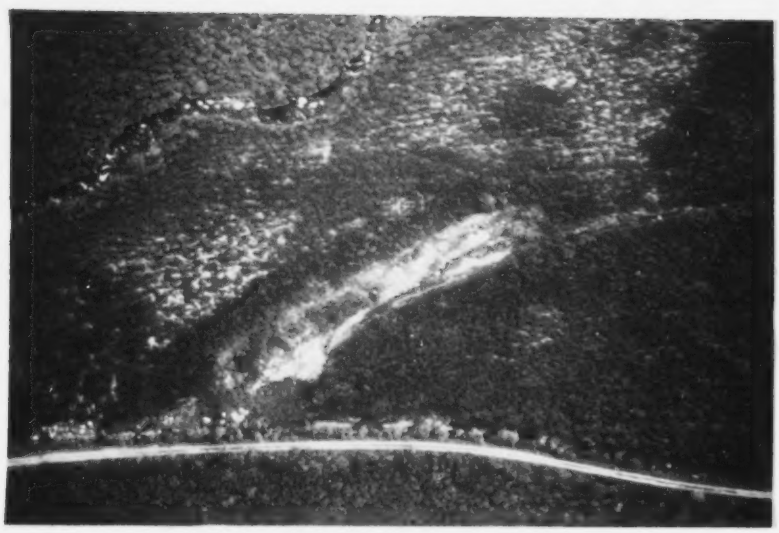

Plate I-10. Photograph taken from an airplane in 1993 of the eastern microclimate station.

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II. PLANT COMMUNITY RESPONSE

Introduction

Studies on natural revegetation in the Arctic have revealed that species composition differs from the surrounding tundra up to 35 years following anthropogenic disturbance (Ebersole and Webber 1983; Kershaw 1983). Often species richness or diversity on disturbed sites is less than on undisturbed areas (Chapin and Shaver 1981; Ebersole and Webber 1983; Bishop and Chapin 1989; Truett and Kertell 1992). Lower values for total plant cover have also been reported on many disturbed sites compared to undisturbed tundra (Bliss and Wein 1972; Bishop and Chapin 1989; Felix and Raynolds 1989; Felix *et al.* 1992).

Plant recovery patterns differ among tundra plant communities (Bliss and Wein 1972; Komarkova 1983; Kershaw 1984). The effects of disturbance, such as the degree of vehicle impact, are partly a function of the type of vegetation (e.g. Rickard and Brown 1974). Tundra shrub communities have been found to be more susceptible to winter track disturbances than wetland sedge communities (Hok 1971; Bliss and Wein 1972). Of the tundra plant communities in the CANOL corridor, Erect Deciduous Shrub Tundra (EDST) suffered the greatest loss of phytomass and had the slowest recovery 35 years following disturbance (Kershaw 1983).

In all tundra plant communities, different relative abundances of species, elimination and introduction of taxa, and changes in cover between disturbed and undisturbed sites are evident even after 30-35 years (Lawson *et al.* 1978; Kershaw 1984; Ebersole 1985; Kershaw and Kershaw 1987). These observations demonstrate that secondary succession in northern environments is still not complete after several decades. Dissimilarity may even be increasing between disturbed and undisturbed tundra as observed in a sedge-shrub tundra community for the first five years following disturbance (Felix *et al.* 1992). Tundra plant community succession is a long process that may still be in the early stages even after several decades.

Svoboda and Henry (1987) describe the rate of succession in the High Arctic as a measure of biological driving forces and environmental resistances. Bliss and Peterson (1992) developed their ideas for anthropogenic disturbances in the Low Arctic by suggesting that secondary succession is a directional change without species replacement. Species establishment and survival become more important in higher latitudes and harsher environmental conditions (Svoboda and Henry 1987; Bliss and Peterson 1992).

Studies on the long-term natural revegetation of disturbed sites are needed to test these succession theories in tundra communities. However, the time scale required by succession necessitates studies that are inferential and

non-experimental without a time-control (Webber and Ives 1978). Although this study lacks a time-control, the general survey done by Kershaw (1983, 1984) in the area fifteen years earlier permits a degree of comparison of two time periods in successional development. Although inferential in nature, such studies still reveal valuable insight beyond the initial stages of tundra succession, that cannot be acquired by any other means.

Such insight into the long-term effects of different types of disturbances is particularly relevant to management issues in the Arctic. Different intensities of disturbance can be thought of as different stages or degrees of succession based on the presence or absence of the original vegetation, organic layer, and any seeds or vegetative propagules. The vegetation and organic layers are removed from primary disturbance substrates such as pits, while some of the original soil remains on vehicle tracks, an example of a secondary succession surface. Borrow pits, bladed trails and vehicle tracks can be considered as points on the continuum from primary to secondary succession.

Revegetation on borrow pits has been considered as primary succession by others (Kershaw and Kershaw 1987; Borgegard 1990). In contrast, unbladed winter roads usually leave an intact organic layer (Hernandez 1973). Bladed trails and concentrated vehicle traffic are considered more intense disturbances (Lawson *et al.* 1978). Different plant community responses to disturbance types (Bliss and Wein 1972; Lawson *et al.* 1978; Kershaw 1984), supports the idea of degrees of succession. Succession is not only affected by species characteristics and interactions (Cargill and Chapin 1987), but also by the initial disturbance conditions.

Succession was investigated in this study by comparing plant species composition on different disturbance types associated with the CANOL pipeline corridor in Erect Deciduous Shrub Tundra (EDST). Different types of succession (primary and secondary) are examined on borrow pits, bladed trails and vehicle tracks. Different stages of succession, 35 and 48 years following abandonment, are examined by comparing results to those from the same location in 1977-79 (Kershaw 1983, 1984).

Emphasis is placed on how different taxonomic groups, especially lichens, respond to disturbance. Taxonomic bias, prevalent in many studies on disturbance in tundra communities (Cox and Larson 1993), is avoided by including all vascular and non-vascular plant species. Taxonomic groups can respond differently to the same environmental variables (Cox and Larson 1993). Lichens are particularly susceptible to disturbance and are often eliminated with no signs of recovery after a few years (Bliss and Wein 1972; Ebersole 1987; Felix *et al.* 1992) or even 3 decades (Ebersole 1985; Kershaw 1983, 1984). Other studies which

focus only on vascular species (e.g. Chapin and Shaver 1981; Ebersole and Webber 1983; Bishop and Chapin 1989) have neglected the importance of bryophytes and lichens during primary and secondary succession in tundra ecosystems.

Methods

Within each site, fifteen random 0.0625 m^2 quadrats (25cm x 25cm) were used to sample herbaceous and non-vascular vegetation. Nails were inserted into the ground in two corners of each quadrat for potential relocation. Cover was estimated for each plant species to the nearest 5% and to the nearest 1% for cover under 10%. Cover of shrubs over 30cm, rock, bare ground, water and litter was also recorded. Additional species found at the site but outside the quadrats were also noted.

Identification of vascular and non-vascular plants to species level was attempted on site. After examination of extensive plant collections, some species were grouped to genera or form due to uncertain identification in the field (e.g. *Antennaria* spp., acrocarpic mosses). Nomenclature follows Porsild and Cody (1980) for vascular plants, and Vitt *et al*. (1988) for bryophytes and lichens; Thompson (1984) was also used for the lichen nomenclature. Hultén (1968) and Hubbard (1955) were useful for the identification of vascular plants and grasses. A voucher collection can be found at the University of Alberta herbarium (ALTA) .

Average cover and frequency values of all species and taxonomic groups were calculated for each site; average cover per site was also determined for shrubs, litter, rock and bare ground. Species richness was determined for different taxonomic groups per quadrat as well as for the entire site (including species found outside the quadrats).

Site values were averaged for undisturbed, pit and linear disturbances. Within disturbance categories, average values were calculated separately for sites east and west of the base camp. Linear disturbance sites were divided into five categories: access roads, bulldozer tracks, bladed trails, multiple tracks, and heavy use tracks (see Introduction - Study Area).

Species with an average cover of greater than 10%, or an average frequency greater than 1% within each disturbance type were considered 'common' on that disturbance type. Frequency was used to compare species abundance on undisturbed areas, borrow pits and linear disturbances.

Univariate nested ANOVAs, performed on Systat (Wilkinson 1992), were used to test whether the variation of the following categories was significantly greater among disturbance types than within disturbance types: cover and species richness for different taxonomic groups; the cover of the dominant species, *Betula glandulosa*; the cover of other genera and taxonomic groups; the cover of litter,

shrub, rock and bare ground. Due to the lack of independence among the tested variables, a multivariate nested ANOVA was performed on SPSS (Nie 1993) using all the above variables. Tukey tests, also performed on Systat (Wilkinson 1992), were used to interpret further the source of variation among the three disturbance types. In addition, differences among categories of linear disturbances were analyzed using nested ANOVAs. All data were log-transformed prior to analysis due to skewed frequency distributions.

Detrended correspondence analysis (DCA), a weighted averaging ordination technique developed by Hill and Gauch (1980), was performed on the species/quadrats data set using ten random quadrats in each site. Species with low frequencies were omitted from the analysis. Species data were transformed with a logarithmic transformation (ln (y+1)) due to the presence of many zeros in the data (as recommended by Ter Braak 1986).

Ordination involves the arrangement of sites and species along axes representing the greatest variation in species composition. The proximity of points may indicate similarity in species composition (Ter Braak 1987b). The ordination axes are often assumed to represent latent or hypothetical environmental variables from an underlying structure in the data (Austin 1985, Ter Braak 1987b, Ter Braak and Prentice 1988). The unimodal species response model used in DCA is appropriate for data sets with wide environmental gradients and community variation (Ter Braak and Prentice 1988). Although detrending can impose a homogenous distribution on the data (Ter Braak 1986), it alleviates the edge and arch effects often observed in correspondence analysis (Ter Braak and Prentice 1988). Detrending by segments (26 segments) with nonlinear rescaling of axes was performed using the CANOCO program (Ter Braak 1988). Plots of the results were produced using CanoDraw LITE (Smilauer 1992), NeoPaint (Riley 1993), PicLab (Crocker 1990) and TerraFirma (Eyton 1994).

Results

Undisturbed shrub tundra

Undisturbed EDST was characterized by a continuous, but sometimes sparse shrub canopy. Litter was prevalent at over 25%; rock and bare ground were both rare (Table II-1). Bryophytes and lichens formed a dense non-vascular mat in the understorey with a combined mean cover of over 100% (Table II-2). Shrubs and decumbent woody species were also abundant covering over 50%. Broad-leaved forbs, graminoids and other plants (*Equisetum* and *Lycopodium* spp.) were minor components of cover in undisturbed shrub tundra.

Most of the 17 species per 625cm^2 quadrat were woody plants, lichens and bryophytes. Less than one species in

each of the forb, graminoid and 'other' categories was present in each quadrat. Within a 200m^2 area, the total number of species was highest for lichens, followed by woody, bryophyte and forb species. Common species included mostly low-growing woody plants, fruticose lichens and pleurocarpic mosses. Some taller shrubs, foliose lichens, broad-leaved forbs and *Equisetum* spp. were also common (Table II-3; Appendices 1, 2).

Undisturbed EDST on the eastern part of the valley had greater average cover and species richness for all taxonomic groups except lichens which had substantially higher values in the western area (Table II-2). Most common woody, forb, grass, bryophyte and *Equisetum* species tended to occur with notably greater frequency or cover on the east slope (Table II-3). *Stereocaulon* spp., *Cladonia* spp., crustose lichens, acrocarpic mosses and *Polytrichum piliferum* were the only common taxonomic groups found with greater cover and frequency in the western sites.

Borrow pits

Most of the sparse total plant cover in borrow pits was comprised of lichens and bryophytes (Table II-2, Plates II-1, II-2). Woody plants were the most abundant vascular taxonomic group but still only covered 10% of the pits. Although the average cover of forbs and graminoids was small, their abundance was still greater than in undisturbed areas (Plate II-3). Borrow pits also had very low cover of shrubs and litter, and very high rock and bare ground cover (Table II-1).

Most of the species within each quadrat were non-vascular. Lichens also comprised a large portion of the species richness per site. In borrow pit sites, forb and woody species were more numerous than bryophytes or graminoids. Eleven of the common species in borrow pits (Table II-4) were also common in undisturbed EDST.

Borrow pits in the eastern region had higher cover values for all taxonomic groups except bryophytes, and greater species richness except for lichens (Plate II-4). Western pits were characterized by bare rock that was six times more abundant than in eastern pits (Plate II-5).

Linear disturbances

Woody plants were almost as abundant on linear disturbances as in undisturbed areas (Table II-2). High species richness of bryophytes and lichens also characterized sites of this disturbance type. Linear disturbances differed from pits and undisturbed areas by their abundance of forbs and graminoids, and high total species richness (Plate II-6). Standing water was most common on linear disturbances (Table II-1). Linear disturbances had numerous common species from all taxonomic

groups (Table II-5).

Generally, species composition did not differ significantly between the various linear disturbance types (nested ANOVAs; Appendices 7, 9). The only exceptions were for the number of broad-leaved forbs, the cover of *Lycopodium* spp. and the number of bryophytes per site.

Heavy-use tracks had greater cover of vascular plants and bryophytes than bulldozer tracks in the western region (Table II-6, Plate II-7). Lichens were more abundant on western bulldozer tracks, which also had more rock and bare ground than any other linear disturbance type (Table II-7).

East of the base camp, multiple track disturbances had the greatest overall plant cover, followed by bulldozer tracks, access roads and bladed trails. Species richness was high for bladed trails and multiple tracks, and low for access roads and bulldozer tracks. Low abundance of bryophytes, and high cover of shrubs and bare ground characterized access roads. Bryophytes were more abundant in bulldozer tracks, where vascular plants, litter and bare rock had low cover. Bladed trails were noteworthy for the occasional presence of water and low cover of woody plants (Plate II-8). Multiple track disturbances had relatively high abundances of vascular plants and bryophytes, and low cover of rock, bare ground and lichens (Plate II-9).

Differences among disturbance types

A total of 151 species (or taxonomic groups) were identified within the study area (Appendices 1-5). The greatest overall plant cover was found in undisturbed sites, although significantly more species were found in linear disturbance sites.

Most of the variables tested by the univariate nested ANOVAs varied significantly among disturbance types. Only some of these variables were still significant in the multivariate ANOVA (Table II-8). Despite log-transformation, the variances for several variables remained unequal among disturbance types (Cochrans and Bartlett-Box, SPSS, Nie 1993).

Woody plants were the only taxonomic group that varied significantly among the three disturbance types in the multivariate ANOVA. The abundance of woody plants decreased from undisturbed areas to borrow pits. Cover of *Betula glandulosa*, the dominant woody species, followed the same trend. Forbs and graminoids were more prevalent on linear disturbances.

Lichen genera and morphological forms of moss exhibited various responses to disturbance: *Cetraria* spp., *Cladina* spp. and pleurocarpic mosses were prevalent in undisturbed sites, while *Stereocaulon* spp., crustose lichens and acrocarpic mosses predominated in borrow pits. The combined effect for lichen abundance was an overall insignificant difference among disturbance types. The number of bryophyte

species was highest in linear disturbances.

Shrub and litter cover both decreased significantly with increasing severity of disturbance. In contrast, rock and bare ground had significantly greater cover in borrow pits than linear disturbances, and had very little cover in undisturbed areas. In borrow pits, almost half of each quadrat was covered by rock and bare ground on the average. Standing water on all sites was rare but most common on vehicle tracks (Table II-1).

Differences among disturbance types based on species composition were also evident in the DCA ordination diagram (Figure II-1). Species composition in linear disturbances was intermediate between pit and undisturbed sites, with overlap of some quadrats with the other two categories. Quadrats from borrow pits, linear disturbances and undisturbed sites are separated along a diagonal in the diagram, but primarily along the first axis which has an eigenvalue of 0.570 (Table II-9). An eigenvalue measures the variance or dispersion of the species' distributions along an axis, and therefore reflects its importance (Ter Braak 1987a, b, 1988).

The second axis, with a relatively high eigenvalue, separates quadrats east of camp from those west of camp. Due to the high total variance, only 14.6% of the species data was explained by the first two axes. Cumulative percentage variance of the species data is the eigenvalues for those axes divided by the sum of all eigenvalues (Ter Braak 1990).

The relationship of linear disturbance types to undisturbed areas and borrow pits is displayed in the ordination diagram (Figure II-2). Points from linear disturbances located within the cloud of points from undisturbed areas are mostly from bulldozer tracks or multiple track disturbances. The species composition on these quadrats is indistinguishable from those in undisturbed shrub tundra. The proximity of points from heavy-use tracks, access roads and bladed trails to those from borrow pits indicate similarities in species composition of these disturbance types.

Species points, positioned approximately in the centre of the points of sites in which they occur (Ter Braak 1990), were concentrated around either undisturbed or borrow pit sites (Figure II-3). Very few species' optimum occurrences were near points from linear disturbances. The affinity of lichen species for the western part of the valley, and of vascular species to the eastern slope is evident. The significantly greater abundance of woody plant species on undisturbed sites is also shown in the diagram.

Linear disturbances had the most common species (54) of any disturbance type. The number of species found with the greatest frequency on linear disturbances (59) was higher than for borrow pits or undisturbed areas (Table II-10).

These were mostly forbs and woody species with very few lichens and no *Cladonia* spp. Ten common species were at least twice as frequent as on other disturbance types. No species common in undisturbed areas were completely absent from linear disturbances.

Most of the 36 species with the greatest frequency in undisturbed areas were lichens and woody species. Twenty-one of these species were common in EDST. The following species were common and at least twice as frequent in undisturbed areas as in either type of anthropogenic disturbance: *Arctostaphylos rubra, Rubus Chamaemorus, Cladonia gonecha, Cladina rangiferina, Cladina stellaris,* and *Parmeliopsis hyperopta*.

Of the 52 species found more often in borrow pits than in linear disturbances or undisturbed areas, 17 were common and at least twice as frequent in pits. Nine other species common on either undisturbed or linear disturbance sites were absent from borrow pit sites (Table II-11).

Discussion

Although an attempt was made to isolate the effects of disturbance type by studying a homogeneous plant community, strong regional variation in species composition was evident in undisturbed shrub tundra. Topography and parent material are the most likely influences through their effects on microclimatic and edaphic conditions. Lichens predominated on well-drained alluvial gravel in the base of the valley; bryophytes and vascular plants were found on glacial till with poorer drainage on the eastern slope.

The regional effect in the data did not override differences in species composition between borrow pits, linear disturbances and undisturbed shrub tundra. The variation among disturbance types occurred along the most important first ordination axis (Figure II-1), and is also supported by several significant differences in the nested ANOVA analyses (Table II-8). Heterogeneity within EDST and a small number of sites may have been factors that contributed to the non-significance of differences among linear disturbance types.

Relative differences in species richness among disturbance types depended on scale. Other studies reported fewer species (Chapin and Shaver 1981) or a reduction in species diversity (Bishop and Chapin 1989) on vehicle tracks and gravel pads. Both these studies omitted non-vascular species and used a small quadrat size or point-intercept methods. At the quadrat level, vascular plant species richness was lower on CANOL disturbed sites. The substantially greater number of species per 200m^2 site in both CANOL pits and tracks demonstrates the importance of scale when investigating species richness.

Different species composition on disturbed sites

compared to the surrounding tundra often accompanied a reduction in species diversity (Ebersole and Webber 1983; Bishop and Chapin 1989; Truett and Kertell 1992). Fewer tundra plant species may be adapted to disturbance conditions, particularly when removal of the organic layer exposes mineral soil. Different plant species require either mineral or organic substrates for seedling establishment (Kershaw 1983).

A decrease in cover on disturbed sites noted in shorter term studies (Bliss and Wein 1972; Bishop and Chapin 1989; Felix *et al.* 1992) is still evident in this long term study. Another study also reported the elimination of species from disturbed areas (Ebersole and Webber 1983; Ebersole 1985). Only nine common species were still absent from borrow pit sites in the study area after almost 50 years, and none were absent from linear disturbances. With increased time since disturbance, it is likely that more species return to the disturbed sites, with fewer species completely excluded. Invasions of species into disturbed areas and increases in cover of individual species reported by other studies (Hernandez 1973; Ebersole 1985) were also common in this investigation as evidenced by the numerous species not found in undisturbed areas (Appendices 1 and 2).

Authors have suggested various causes for low cover and species diversity on disturbances in arctic communities. A decrease in soil moisture from changes in particle size composition and drainage patterns can restrict germination on disturbed sites (Brady 1984; Kershaw 1984; Bishop and Chapin 1989; Borgegard 1990). Temperature and nutrient availability have also been associated with revegetation of northern disturbed sites (Ebersole and Webber 1983; Bishop and Chapin 1989; Borgegard 1990; Truett and Kertell 1992). For a more complete discussion of the relation of abiotic factors to revegetation of disturbed sites, refer to Chapter IV.

Buried seed and seed dispersal into disturbed areas are some of the major biotic factors controlling natural revegetation (Gartner *et al.* 1983). The reduced buried seed supply on mineral substrates can often limit recovery on disturbed sites (Gartner *et al.* 1983; Cargill and Chapin 1987; Ebersole 1989). With few buried seeds left in some disturbed soils, a limited seed dispersal has been found to cause low cover and species diversity (Bishop and Chapin 1989).

Comparison of revegetation on different types of disturbance

Major differences between revegetation on borrow pits and linear disturbances even 48 years following abandonment illustrate the differences between primary and secondary succession in shrub tundra communities. Almost fifty years of primary succession on CANOL borrow pits in EDST resulted in a fundamentally different plant species composition than

the surrounding undisturbed areas. A few shrubs and broad-leaved forbs were scattered in the disturbance plant community dominated by *Stereocaulon* spp., crustose lichens and acrocarpic mosses.

In western pits with very few shrubs and a sparse cover of *Stereocaulon* spp., recovery is very slow; it could take centuries before any substantial change in species composition is observed. Total cover and number of vascular plant species on western CANOL pits resembled a gravel site only eight growing seasons following disturbance (2.7% total vascular plant cover and 4.6 species, Bishop and Chapin 1989). In pits on the east slope, the development of a discontinuous shrub canopy will likely lead to changes in the micro-environment and the establishment of a *Cladina*/pleurocarpic moss understorey within the next century.

Low cover of vascular plants on CANOL borrow pits can be partly attributed to the low seed dispersal and lack of buried seed and organic matter. Recovery on other primary succession sites has also been limited by a lack of organic soil, few buried seeds and xeric conditions (Gartner *et al.* 1983; Cargill and Chapin 1987; Ebersole 1989). Seeds that disperse into the disturbance from the immediate surrounding area are usually poorly adapted to disturbance conditions. Instead, seeds adapted to the disturbance micro-environment generally come from natural disturbances or other gravel areas (Cargill and Chapin 1987). The source of these seeds in the CANOL study area may be other plant communities, riparian gravel areas, or permafrost-related natural disturbances.

Plant cover was still greater on undisturbed areas than on CANOL linear disturbances after 48 years. In a shrub-sedge tundra community, Bliss and Wein (1972) also noted a decrease in plant cover on seismic lines. The vigorous growth of forbs and graminoids on CANOL vehicle tracks is more comparable to studies done in tundra not dominated by shrubs. For example, in graminoid-dominated tussock tundra, more vigorous plant growth was reported on vehicle tracks after 1-10 years (Chapin and Shaver 1981). Ebersole (1985) observed the elimination of some species on partially disturbed vehicle tracks. Any species common in undisturbed areas that would have been eliminated from CANOL linear disturbances in the study area, had reinvaded by 1993.

On linear disturbances west of the base camp, greater abundance of vascular plants, especially woody species, infers that heavy-use tracks are at a later stage of succession than bulldozer tracks. In another study, multiple-pass trails (heavy-use tracks) were some of the most intense disturbances (Lawson *et al.* 1978). The unexpected result in the present study may be due to topography. The more intensely used tracks were generally found at lower elevations and would have been less exposed

to wind and moisture loss. The greater abundance of *Stereocaulon* spp. on heavy-use tracks, a genus commonly associated with disturbances, suggests that initially these tracks were more intensely disturbed than other western bulldozer tracks.

On eastern vehicle tracks, there is an apparent increasing intensity of disturbance: multiple tracks < bulldozer track < pit access road < bladed trail (from least to most intense). Cover of woody plants decreases with disturbance intensity according to this pattern. The degree of disturbance is largely a function of the impact of the removal or alteration of the pre-disturbance vegetation and soil (see Introduction - Study Area). Multiple track disturbances often had less impact than a typical bulldozer track since the tracks were usually only single-pass tracks. Bladed trails were the most intense linear disturbances since most of the organic soil layer was bladed away. Ebersole and Webber (1983) and Lawson *et al.* (1978) also found that bulldozing (blading) was the most severe and lasting disturbance.

Lichen cover increases with disturbance intensity following the same pattern. Initially this would suggest that lichen cover decreases with succession, an idea which is not supported by greater lichen cover in undisturbed areas. Different lichen species are prevalent in disturbed and undisturbed communities. *Stereocaulon* spp. and *Peltigera* spp. comprised most of the lichen cover on vehicle track sites. Cover of lichen species found primarily in undisturbed EDST (e.g. *Cladina* spp.) may only substantially increase in the later stages of succession.

Other taxonomic groups do not follow the trend of increasing disturbance intensity as indicated above. Other factors such as compaction, surface material and drainage would also have influenced secondary succession on linear disturbances.

Part of the variation in species composition on different types of linear disturbances can be attributed to the effect of partial removal of the organic layer on the buried seed pool. More than half of all seeds, and 90% of all dicotyledonous seeds germinated from the top 5cm of soil in a study in tussock tundra (McGraw 1980). Ebersole (1989) also found more taxa and seeds in the top 5cm of soil. If this layer is bladed away, as in bladed trails, fewer seeds are available for revegetation (Gartner et al. 1983; Cargill and Chapin 1987), as evidenced by lower cover of vascular plants on CANOL bladed trails than other linear disturbances.

Comparison to revegetation 35 years following abandonment

A thorough indirect comparison of species composition on disturbed sites in EDST between 1978 and 1993 (33 and 48 growing seasons following abandonment) elucidates patterns

of long-term revegetation of borrow pits and linear disturbances associated with the CANOL pipeline corridor (Table II-12). All of the 1978 data are from either the *Betula glandulosa - Cladina stellaris* - moss community or all the sites in EDST from Kershaw (1983, 1984).

Methodology and site locations differed between the two studies. The 1978 study included 8 locations within the 1993 study area, as well as 66 additional locations further east. Most of the locations in EDST from 1978 resembled the vegetation in the western part of the 1993 study area (Kershaw pers. comm.). The sampling unit in 1978 was 0.5m x 5.0m which is between the size of the quadrat and site used in 1993. The numbers of sites in each disturbance type are comparable between the two studies (Table II-12).

The change in the cover of bare ground is an indication of the increase of total plant cover in successional development. Although greater total plant cover was recorded on all borrow pits in 1993 than in 1978, the amount of bare ground on western pits appears to have increased from 1978 to 1993. The magnitude of the reduction in bare ground on eastern pits and all types of linear disturbances infers a notable increase in total vegetative cover on all CANOL disturbances in this stage of successional development. A nearly complete plant cover may be established on vehicle tracks within the next few decades, and on eastern borrow pits within the next century. Pits west of camp with 75% cover of rock and bare ground in 1993 may take centuries to revegetate.

Despite different sample sizes and methodologies, it can be concluded that species richness on CANOL disturbances increased from 1978 to 1993. Much greater numbers of species per site in disturbances (except in western pits) than in undisturbed areas were found in 1993; whereas Kershaw generally observed fewer species on the disturbed sites than in controls. With successional development, more species are invading borrow pits and linear disturbances.

Unfortunately, changes in the abundances of individual species from 1978 to 1993 could not be determined since Kershaw only reported differences in cover and not actual cover values. The relative abundances of the common species among the different disturbance types mostly remained the same. Species that had significantly greater cover on borrow pits and/or linear disturbances in 1978 were also prevalent on disturbed sites in 1993. These included mostly graminoids and terricolous lichens.

Other species were found with greater cover in undisturbed areas at both 33 and 48 years following abandonment. These woody plants and *Cladina* spp. may only establish comparable levels of cover on disturbed sites in the later stages of succession; they may be good indicator species of undisturbed EDST. Higher frequencies of both *Betula glandulosa* and *Salix reticulata* on linear

disturbances in 1993 suggest that woody EDST species had been invading linear disturbances and were beginning to establish cover similar to that in undisturbed EDST. *Cladina* spp. with relatively low frequencies in 1993, may take centuries to form a dense understorey mat beneath a *Betula* canopy.

Species which differ in relative abundances on disturbed and undisturbed sites from 1978 to 1993 are particularly noteworthy. *Antennaria* spp., *Cetraria islandica* and *Polytrichum strictum* had greater cover on undisturbed areas than some linear disturbances (Table II-12) in 1993, but not in 1978. These species may be more abundant in the earlier stages of succession, or the differences may simply be an artifact of different sampling sites.

Although *Artemisia arctica* had significantly greater cover on undisturbed areas in 1978, it was more abundant on both bulldozer tracks and borrow pits in 1993. *A. arctica* may be a good candidate for an indicator species of the later stages of successional development in shrub tundra.

In 1978, *Stereocaulon paschale* was more abundant in the control rather than the disturbed samples. Although all *Stereocaulon* spp. were grouped together for the 1993 data, later identification revealed that most *S. paschale* were found in undisturbed sites and most *S. alpinum* were found on disturbed sites. Substantially greater cover of *Stereocaulon* spp. on all disturbance types in 1993 suggest that its abundance was increasing on CANOL disturbances.

Similarities in species composition between undisturbed and disturbed areas in 1978 and 1993 suggest that succession was proceeding very slowly in EDST in the CANOL corridor. However, the decrease in the cover of bare ground, and the increase in species richness provide evidence for greater revegetation in the last fifteen years, particularly on linear disturbances. The changes in abundance of individual species on disturbed areas may indicate the affinity of these species for particular stages of succession.

Due to different sampling locations and methodology, these conclusions remain inferential and any predictions would be hypothetical. Measures were taken in the 1993 study to make it possible to replicate the same study in another fifteen years which would reveal substantially more insight into primary and secondary succession in the CANOL corridor.

Revegetation patterns of different taxonomic groups and species

Early colonizer vascular plant species are usually light-seeded with high dispersal capacities (Lawson *et al.* 1978; Cargill and Chapin 1987). Examples of woody pioneer species include *Salix* spp. which are high-turnover species that grow rapidly and produce abundant light seed (Ebersole

and Webber 1983; Cargill and Chapin 1987; Bliss and Peterson 1992). *S. alaxensis, Salix glauca, S. planifolia, S. lanata, S. myrtillifolia* and *S. reticulata* successfully colonized gravel pads, glacial outwash, riparian gravel bars, borrow pits, bladed surfaces, and/or mounds of soil (Ebersole and Webber 1983; Ebersole 1987; Kershaw and Kershaw 1987; Bishop and Chapin 1989). The greater abundance of *Salix* spp. on some of the CANOL linear disturbances indicates an intermediate stage in succession; these species have not yet been replaced species characteristic of the undisturbed *Betula glandulosa* community.

Several studies have found that linear disturbances reduce or eliminate ericaceous shrubs (Chapin and Shaver 1981; Ebersole 1985). *Vaccinium vitis-idaea*, considered highly sensitive to disturbance (Felix and Raynolds 1989), was absent from most tracks (Chapin and Shaver 1981), as well as the first two stages of primary succession in a glacial outwash area (Viereck 1966). However, *V. vitis-idaea* was present on another 4-year old disturbed site (Ebersole 1987). *V. uliginosum* and a non-ericaceous shrub, *Empetrum nigrum*, were absent in other disturbances and primary succession sites (Viereck 1966; Chapin and Shaver 1981). These understorey shrubs were either present in low cover on all types of disturbance or even more abundant on linear disturbances. Comparison with the above short-term disturbance studies suggests that ericaceous shrubs increase in abundance with successional development.

Although forbs were absent from 30-year old disturbed sites in another area (Ebersole 1985), 48 years after abandonment of CANOL disturbances, broad-leaved forbs were more plentiful on almost all types of disturbance than in undisturbed areas. No nitrogen-fixing legumes, often important colonizers in other areas (Viereck 1966; Cargill and Chapin 1987; Bishop and Chapin 1989), were found on any of the sites (disturbed or undisturbed) with the exception of *Astragalus umbellatus* that was very rare on linear disturbances. Borgegard (1990) also observed that the most frequent pioneers on newly abandoned pits were not nitrogen-fixers.

Competition for light can contribute to successional development patterns in shrub communities (Bliss and Peterson 1992). With a decrease in shrub cover on disturbed sites, increased availability of light would favour the establishment of broad-leaved forbs. Forbs would also have had less competition from mosses on disturbed sites which can out-compete vascular plants (Bliss and Peterson 1992).

The rapid recovery of graminoids on disturbed sites was also observed in other studies (Bliss and Wein 1972; Chapin and Shaver 1981). *Poa* spp. and *Trisetum spicatum*, successful colonizing grasses on disturbed tundra sites (Viereck 1966; Ebersole and Webber 1983; Ebersole 1987;

Kershaw and Kershaw 1987), were also present on CANOL disturbed sites. *Carex aquatilis*, one of the species found twice as frequently on linear disturbances than on borrow pits or undisturbed sites, was also prevalent in bulldozed areas and other, usually wet, disturbances (Lawson *et al.* 1978; Ebersole and Webber 1983; Ebersole 1987).

Different revegetation patterns of vascular and non-vascular species illustrate the importance of including all taxonomic groups in succession studies in order to avoid taxonomic bias. Lichens had opposing trends to other plant species; they were the only distinguishable taxonomic group in the ordination diagrams. Lichens are particularly relevant to long-term revegetation on disturbed sites due to their susceptibility to disturbance and lengthy re-establishment period (Bliss and Wein 1972; Ebersole 1987; Felix and Raynolds 1989).

Despite reports of slow recovery of lichens on disturbed sites (Bliss and Wein 1972; Ebersole 1985), Viereck (1966) reported a mat of *Stereocaulon* spp. on 30-year old glacial outwash. Results after 48 years of natural revegetation on CANOL sites also provide evidence for the recovery of lichens, particularly *Stereocaulon* spp., on all disturbances, especially eastern borrow pits.

Lichen species respond differently to disturbance. *Cladina rangiferina, C. stellaris* and *Cladonia sulphurina* could be considered vulnerable to disturbance since they were common and at least twice as frequent in undisturbed areas as in disturbances. Other species such as *Stereocaulon* spp., some *Cladonia* spp., saxicolous and crustose lichens, were much more prevalent on borrow pits. Some of these were also identified by Kershaw and Kershaw (1987) as successful in colonizing borrow pits: *Cladonia cariosa, Psoroma hypnorum* and *Stereocaulon tomentosum*.

Bryophytes were also reported to have slow recovery and high susceptibility to disturbance (Bliss and Wein 1972; Ebersole 1985; Felix and Raynolds 1989). Viereck (1966) reported a nearly continuous mat of moss by the second stage of succession, 100 years after deglaciation. Bryophyte cover on CANOL linear disturbances in 1993 was similar to undisturbed shrub tundra, but borrow pits still had less than a third of the cover of undisturbed sites. Most of the bryophyte cover in the western pits was comprised of *Polytrichum piliferum*. Another successful colonizer of borrow pits, *Rhacomitrum canescens*, was also found on the first successional stage of an outwash plain (Viereck 1966). *Dicranum* spp. are considered highly sensitive to disturbance by Felix and Raynolds (1989) and were rarely found in CANOL pits.

Succession in Low Arctic shrub tundra ecosystems

Similarities with the pioneer stage on glacial outwash (Viereck 1966), and other disturbed sites shortly following

disturbance (e.g. Bishop and Chapin 1989), imply that CANOL borrow pits, particularly the western ones, were still in the very early stages of succession. Revegetation was proceeding faster on some eastern pits where *Stereocaulon* spp. had formed a more extensive cover. On all CANOL pits the development of a dense canopy of *Betula glandulosa* and an understorey mat of *Cladina* spp. and pleurocarpic mosses will probably require many centuries. Ebersole and Webber (1983) also found no evidence of the next successional stage in their study of bulldozed mounds 30 years following disturbance.

Linear disturbances, even multiple tracks which superficially resembled undisturbed shrub tundra, were still in the intermediate stage as revealed by the persistence of pioneer species (e.g. *Salix* spp.). Further evidence of the continued succession is provided by the increase in species richness from 1978 to 1993 on CANOL linear disturbances.

During successional development, species establishment and survival, considered more important than species replacement in the High Arctic (Svoboda and Henry 1987; Bliss and Peterson 1992), also dominate the earlier successional stages in the Low Arctic. In CANOL borrow pits, species replacement had not yet been observed by 1993, as illustrated by the persistent bare ground and greater abundance of numerous species in pits in both 1978 and 1993. Although succession in the Low Arctic is expected to be a directional change with species replacement (Bliss and Peterson 1992), the time scale may be so great for primary succession sites that it may take centuries to observe.

Bliss and Peterson (1992) predict that secondary succession with directional change and without species replacement predominates in anthropogenic disturbances in all habitats. However, because of different species composition on CANOL linear disturbances and undisturbed EDST, species replacement must eventually occur for the re-establishment of the *Betula glandulosa* community. Differences in relative abundances of some species on CANOL linear disturbances from 1978 to 1993 (e.g. *Artemisia arctica*), provide evidence of the initial stages of species replacement in secondary succession.

The possibility exists that plant communities on CANOL disturbed areas will never resemble undisturbed EDST. Webber and Ives (1978) have suggested that in some areas, complete recovery of disturbed sites may be impossible since the tundra vegetation is in equilibrium with the past, not the present climate. Other studies have predicted time periods of a few decades (Webber and Ives 1978), and several hundred years (Ebersole and Webber 1983; Komarkova 1983) for successional development in the Low Arctic.

Conclusions

Forty-eight years following abandonment of the CANOL pipeline, total plant cover and the abundance of woody plants was significantly higher in undisturbed shrub tundra than in borrow pits or linear disturbances. Species richness per site was greater on both types of disturbance. Despite regional variation, differences in species composition among disturbances types were more important.

CANOL borrow pits, especially western ones, were still in the preliminary stages of succession with persistent bare ground and rock, and a sparse shrub canopy. Pioneer species such as *Antennaria* spp., *Stereocaulon* spp. and acrocarpic mosses had established. Species replacement was not yet apparent in these pits but would have to occur for the re-establishment of the *Betula glandulosa* community. Complete revegetation of these pits may take centuries.

Indications of species replacement on linear disturbances are apparent from the comparison with a similar study of plant communities on CANOL disturbances 15 years earlier (Kershaw 1983, 1984). The relative abundance of several species among disturbance types (e.g. *Artemisia arctica*) had changed during successional development from 1978 to 1993. The persistence of pioneer species such as *Salix* spp. implies that the plant communities are still in the intermediate stages of succession on CANOL vehicle tracks.

Despite differences in plant species composition among linear disturbance types, differences in abundance of various taxonomic groups were generally not significant. However, cover of woody plants decreased with increasing intensity of disturbance, while the cover of lichen species increased.

This study investigated a later stage of succession than most other studies of disturbance in tundra plant communities. The results provide more evidence that primary and secondary succession, even in the Low Arctic, are very slow processes; it could take centuries for the establishment of the *Betula glandulosa* community on the disturbed sites. Forty-eight years following abandonment of the CANOL pipeline, plant communities on borrow pits and linear disturbances in erect deciduous shrub tundra are still only in the early and intermediate stages of succession. Even long-term disturbance studies such as this one can only begin to understand some of the processes beyond the initial stages of establishment in successional development in tundra plant communities.

Table II-1. Average cover (%) of standing water, shrubs over 30cm, litter, rock and bare ground for undisturbed areas, borrow pits and linear disturbances. Data within each disturbance type are also subdivided between eastern and western sites.

	Undisturbed			Borrow Pits			Linear Disturbances		
	East	West	All	East	West	All	East	West	All
n	150	105	255	120	90	210	165	60	225
water	0	0	0	1	0	1	2	0	1
shrub	26	24	25	5	1	4	21	16	20
litter	29	27	29	8	2	5	26	29	27
rock	0	0	0	10	60	32	2	3	3
ground	0	2	1	16	15	15	3	7	4

n = number of quadrats

Table II-2. Average cover, number of species per quadrat and per site for different taxonomic groups in undisturbed areas, borrow pits and linear disturbances. Data within each disturbance type are also subdivided between eastern and western sites.

	Undisturbed			Borrow Pits			Linear Disturbances		
	East	West	All	East	West	All	East	West	All
average cover (%)									
woody plants	66	39	55	16	2	10	55	42	51
forbs	4	0	3	8	1	5	8	5	7
graminoids	2	1	2	4	0	3	4	1	3
lichens	17	64	37	38	18	29	15	33	20
bryophytes	78	45	65	18	18	18	57	51	56
other plants	2	0	1	2	0	1	3	0	2
Total	**170**	**149**	**161**	**86**	**39**	**66**	**142**	**133**	**140**
average # of species per quadrat									
woody plants	8	4	7	2	0	1	4	3	4
forbs	1	0	1	3	0	2	3	1	2
graminoids	1	1	1	2	0	1	2	1	1
lichens	3	7	5	4	5	5	3	6	4
bryophytes	4	3	3	3	2	2	4	3	4
other plants	1	0	1	0	0	0	1	0	1
Total	**19**	**14**	**17**	**14**	**8**	**11**	**17**	**14**	**16**
total # of species per site									
woody plants	10	8	9	10	5	8	11	9	10
forbs	7	2	5	13	3	9	12	7	11
graminoids	2	2	2	7	3	6	5	4	5
lichens	11	14	12	14	15	14	13	21	15
bryophytes	10	6	8	8	5	6	11	9	10
other plants	2	0	1	3	1	2	3	2	3
Total	**41**	**32**	**37**	**54**	**32**	**45**	**55**	**51**	**54**

Table II-3. Average cover and frequency for species with >1% cover or 10% frequency in undisturbed sites. Data are subdivided between eastern and western sites. Some species are grouped together into genera or other taxonomic groups. Species abbreviations are listed in Appendix 5.

	average cover (%)			average frequency (%)		
	East	West	All	East	West	All
woody plants						
Arctostaphylos rubra	3	0	2	12	0	7
Betula glandulosa	25	30	27	89	89	89
Cornus canadensis	1	0	1	21	9	16
Empetrum nigrum	14	4	10	65	15	45
Rubus Chamaemorus	1	0	1	36	4	23
Salix arb. x plan.	3	0	2	15	0	9
Salix reticulata	6	0	4	23	0	13
Vaccinium uliginosum	8	0	5	45	3	27
Vaccinium vitis-idaea	2	3	2	79	89	83
forbs						
Petasites frigidus	1	0	1	21	0	12
forb sp.1	1	0	0	18	0	11
graminoids						
grass spp.	1	1	1	74	47	63
lichens						
Cetraria islandica	0	1	0	5	23	12
Cetraria nivalis	0	2	1	0	31	13
Cetraria pinastri	1	1	1	85	73	80
Cladina arbuscula	1	3	2	11	36	22
Cladina rangiferina	4	7	5	38	48	42
Cladina stellaris	4	32	15	21	83	47
Cladonia sulphurina	0	0	0	3	22	11
Cladonia uncialis	0	1	1	4	23	12
Cladonia tapered	1	3	2	39	83	57
Cladonia cup	0	0	0	8	14	11
Nephroma arcticum	2	0	1	7	2	5
Parmeliop. hyperopta	1	2	2	83	72	78

Peltigera aphthosa	2	0	**1**	15	1	**9**
Stereocaulon spp.	0	5	**2**	1	25	**11**
crustose	0	3	**1**	0	14	**6**
bryophytes						
Aulacomnium palustre	9	0	**5**	50	2	**30**
Dicranum spp.	2	6	**3**	31	51	**40**
Hylocomnium splendens	17	0	**10**	52	0	**31**
Pleurozium schreberi	15	18	**16**	54	43	**49**
Polytrichum com./jun.	10	13	**11**	43	70	**54**
Polytrichum strictum	7	5	**6**	34	40	**36**
Sphagnum spp.	11	0	**6**	35	0	**21**
Tomenthypnum nitens	4	0	**3**	18	0	**11**
liverwort	3	2	**3**	41	46	**43**
other plants						
Equisetum scirpoides	0	0	**0**	33	0	**20**
Equisetum sylvaticum	2	0	**1**	50	0	**29**

Table II-4. Average cover and frequency for species with >1% cover or 10% frequency in borrow pits. Data are subdivided between eastern and western sites. Some species are grouped together into genera or other taxonomic groups. Species abbreviations are listed in Appendix 5.

	average cover (%)			average frequency(%)		
	East	West	All	East	West	All
woody plants						
Betula glandulosa	7	1	4	54	8	34
Empetrum nigrum	3	0	2	21	0	12
Salix plan./glau.	4	1	3	53	14	37
Sibbaldia procumbens	1	0	1	28	2	17
Spiraea beauverdiana	0	0	0	19	0	11
forbs						
Antennaria spp.	2	0	1	48	2	28
Artemisia arctica	2	0	1	21	3	13
Epilobium anagallid.	0	0	0	38	0	21
Epilobium angust.	1	0	1	28	8	19
Pyrola spp.	1	0	0	18	0	10
Sagina Linnaei	1	0	1	40	0	23
Senecio spp.	0	0	0	21	0	12
Veronica Wormskjoldii	1	0	0	37	0	21
graminoids						
Agrostis scabra	2	0	1	55	1	32
grass spp.	0	0	0	18	16	17
Trisetum spicatum	0	0	0	31	1	18
lichens						
Cetraria pinastri	0	1	0	4	50	24
Cladonia cariosa	0	0	0	10	13	11
Cladonia cervicornal.	1	0	1	39	11	27
Cladonia macrophylla	0	0	0	10	14	12
Cladonia tapered	1	1	1	52	47	50
Cladonia cup	1	1	1	62	54	59
Pannaria pezizoides	0	0	0	24	1	14
Peltigera aphthosa	2	0	1	14	11	13

Psoroma hypnorum	0	1	**1**	19	18	**19**
Solorina crocea	1	0	**0**	16	12	**14**
Stereocaulon spp.	25	6	**17**	76	79	**77**
crustose	6	3	**5**	71	71	**71**
bryophytes						
Dicranum spp.	0	0	**0**	19	2	**12**
Drepanocladus sp.1	3	0	**2**	8	0	**4**
Polytrichum com./jun.	2	4	**3**	43	53	**48**
Polytrichum piliferum	1	12	**6**	26	58	**40**
Rhacomitrum canescens	3	0	**2**	18	8	**13**
acrocarpic moss	3	2	**3**	66	67	**66**
liverwort	3	0	**2**	48	1	**28**
other plants						
algae	2	0	**1**	21	0	**12**

Table II-5. Average cover and frequency for species with >1% cover or 10% frequency in linear disturbances. Data are subdivided between eastern and western sites. Some species are grouped together into genera or other taxonomic groups. Species abbreviations are listed in Appendix 5.

	average cover (%)			average frequency(%)		
	East	West	All	East	West	All
woody plants						
Betula glandulosa	19	17	18	84	77	82
Cornus canadensis	1	1	1	13	23	16
Empetrum nigrum	12	14	12	56	43	53
Rubus acaulis	1	0	0	28	0	21
Salix arb. x plan.	2	0	2	12	3	10
Salix lanata	2	0	1	6	0	4
Salix plan./glau.	5	5	5	39	30	37
Salix reticulata	5	0	3	22	0	16
Sibbaldia procumbens	0	3	1	12	33	18
Spiraea beauverdiana	1	0	1	18	7	15
Vaccinium uliginosum	6	1	4	36	17	31
Vaccinium vitis-idaea	1	1	1	51	40	48
forbs						
Artemisia arctica	3	3	3	26	32	28
Epilobium angust.	1	0	1	12	3	22
Petasites frigidus	1	0	1	24	8	20
Polemonium acutiflor.	0	0	0	15	3	12
Pyrola spp.	0	0	0	16	12	15
Stellaria mon./long.	0	0	0	19	7	16
Veronica Wormskjoldii	0	0	0	21	3	16
forb sp.1	0	0	0	16	0	12
graminoids						
Agrostis scabra	0	0	0	13	12	12
Carex aquatilis	1	0	0	20	2	15
Carex spp.	0	0	0	16	7	14
grass spp.	2	1	2	72	57	68
Luzula parviflora	0	0	0	18	5	15

lichens						
Cetraria islandica	0	2	1	4	43	15
Cetraria pinastri	1	0	0	45	40	44
Cladina arbuscula	0	1	0	9	23	13
Cladina rangiferina	1	1	1	15	23	17
Cladina stellaris	1	8	3	14	45	22
Cladonia tapered	1	2	1	37	75	47
Cladonia cup	0	1	0	19	55	29
Parmeliop. hyperopta	1	1	1	34	27	32
Peltigera aphthosa	4	1	3	23	20	22
Solorina crocea	0	3	1	3	40	13
Stereocaulon spp.	3	11	5	25	62	35
crustose	1	2	1	12	27	16
bryophytes						
Aulacomnium palustre	10	0	7	62	5	47
Dicranum spp.	1	3	2	28	28	28
Drepanocladus sp.2	2	3	2	25	10	21
Hylocomnium splendens	8	0	6	43	2	32
Pleurozium schreberi	6	7	7	31	35	32
Polytrichum com./jun.	6	15	8	44	77	53
Polytrichum piliferum	0	5	1	7	33	14
Polytrichum strictum	2	1	2	19	18	19
Rhizomnium spp.	2	0	1	16	0	12
Sphagnum spp.	3	0	2	18	0	13
Tomenthypnum nitens	4	0	3	21	0	16
pleurocarpic spp.	2	0	2	25	0	18
acrocarpic moss	1	1	1	26	40	30
liverwort	10	15	11	66	73	68
other plants						
Equisetum arvense	0	0	0	30	0	22
Equisetum scirpoides	0	0	0	21	0	16
Equisetum sylvaticum	1	0	1	41	0	30

Table II-6. Average cover, number of species per quadrat and per site for different taxonomic groups for different types of linear disturbances.

	Linear Disturbances						
	East				West		
	Access	Track	Bladed	Multi	Track	Heavy	All
average cover (%)							
woody plants	52	63	39	70	22	62	51
forbs	13	3	8	10	1	8	7
graminoids	4	3	4	6	1	1	3
lichens	17	14	21	5	38	27	20
bryophytes	36	75	46	80	41	62	56
other plants	3	2	3	3	0	1	2
Total	**125**	**159**	**121**	**175**	**104**	**161**	**140**
average # of species per quadrat							
woody plants	4	5	4	4	2	4	4
forbs	3	1	3	3	0	2	2
graminoids	1	1	2	2	1	1	1
lichens	3	3	4	2	7	5	4
bryophytes	3	5	5	5	4	3	4
other plants	1	1	1	2	0	0	1
Total	**15**	**17**	**17**	**18**	**14**	**15**	**16**
total # of species per site							
woody plants	12	10	10	13	8	10	10
forbs	12	11	11	16	5	9	11
graminoids	5	5	6	5	3	5	5
lichens	13	13	19	7	22	20	15
bryophytes	9	10	12	12	9	10	10
other plants	2	3	3	4	1	2	3
Total	**52**	**52**	**61**	**55**	**47**	**55**	**54**

Table II-7. Average cover (%) of standing water, shrubs over 30cm, litter, rock and bare ground for different types of linear disturbances.

	Linear Disturbances						
	East				West		
	Access	Track	Bladed	Multi	Track	Heavy	All
n	45	45	45	30	30	30	225
water	0	1	6	0	0	0	1
shrub	27	11	21	27	9	23	20
litter	31	15	27	37	21	36	27
rock	4	0	5	0	6	1	3
ground	4	4	3	1	11	3	4

n = number of quadrats

Table II-8. Summary of results from univariate and multivariate nested analyses of variance (ANOVAs) and Tukey multiple comparisons for average cover and species richness of various taxonomic groups, as well as cover of shrub, litter, rock and bare ground. Only categories significant in either the univariate or multivariate ANOVAs or both are included. The table indicates in which disturbance types the least, moderate and greatest values occur. Categories that were significantly different from one another are indicated by *, ** and ***. The last column indicates the tests (univariate or multivariate) in which the category was significant. All categories are for percent cover except for the number of species. All significance levels are at $p<0.05$. Also see Tables II-1, II-2 and Appendices 1, 6, 8, 10.

U = undisturbed
L = linear disturbances
P = borrow pits
u = univariate
m = multivariate
# = number of species

	least	moderate	greatest	sign.
Total cover	*P	**L	***U	u, m
Total # per quadrat	**P	*L	*U	u, m
Total # per site	*U	*P	**L	u, m
Woody plants	*P	**L	***U	u, m
# woody species per quadrat	*P	**L	***U	u, m
Betula glandulosa	*P	**L	***U	u, m
Broad-leaved forbs	*U	**P	***L	u
# forbs per quadrat	*U	**P	***L	u
# forbs per site	*U	P	**L	u, m
# graminoids per quadrat	*U	*P	**L	u
# graminoids per site	**U	*L	*P	u, m
Cetraria spp.	*P	**L	***U	u
Cladina spp.	*P	**L	***U	u
Peltigera spp.	*P	*U	**L	u
Stereocaulon spp.	*U	**L	***P	u
Crustose lichens	*U	*L	**P	u, m
Bryophytes	**P	*L	*U	u
# bryophytes per quadrat	*P	**U	***L	u
# bryophytes per site	*P	*U	**L	u, m
Acrocarpic moss	*U	**L	***P	u, m
Pleurocarpic moss	*P	**L	***U	u, m
# other spp. per site	*U	P	**L	u, m
Equisetum spp.	**P	*L	*U	u
Lycopodium spp.	*U	*P	**L	u
Shrub cover >30 cm	*P	**L	***U	u, m
Litter	*P	**L	***U	u, m
Rock	*U	**L	***P	u, m
Bare ground	*U	**L	***P	u, m

Table II-9. Results from the DCA ordination of species composition. Eigenvalues indicate the dispersion of the species distributions along an axis, and therefore reflect their importance (Ter Braak 1987a, b, 1988). Cumulative percentage variances of the species data are the eigenvalues divided by the total variance in the species data, also called the total inertia (Ter Braak 1990).

	Axis 1	Axis 2	Axis 3	Axis 4	total inertia
eigenvalues	0.570	0.357	0.176	0.156	6.391
cumulative variance	8.9	14.5	17.3	19.7	

Table II-10. Species found in the greatest frequency in undisturbed areas, borrow pits and linear disturbances. Some species are grouped together into genera or other taxonomic groups. Species common in the respective disturbance type (*) and those that are common and at least twice as frequent (**) are noted. Species abbreviations are listed in Appendix 5.

Undisturbed EDST	Borrow Pits	Linear Disturbances
woody plants		
**Arctostaphylos rubra	Populus balsamifera	*Empetrum nigrum
*Betula glandulosa	Salix alaxensis	Ledum spp.
Cassiope tetragona	Salix arbusculoides	Potentilla fruticosa
*Cornus canadensis	Salix arctica	**Rubus acaulis
Picea glauca	Salix commutata	*Salix arb. x plan.
**Rubus Chamaemorus		**Salix lanata
*Vaccinium vitis-idaea		*Salix plan./glau.
		*Salix reticulata
		Salix sp.
		*Sibbaldia procumbens
		*Spiraea beauverdiana
		*Vaccinium uliginosum
forbs		
Linnaea borealis	**Antennaria spp.	Anemone narcissiflora
Pedicularis labrador.	Arnica Lessingii	Anemone parviflora
	Aster sibiricus	Anemone Richardsonii
	Cerastium Beeringia.	**Artemisia arctica
	**Epilobium anagallid.	Artemisia Tilesii
	Epilobium latifolium	Astragalus umbellatus
	Gentiana sp.	*Epilobium angust.
	Parnassia Kotzebuei	Mertensia paniculata
	Polygonum viviparum	Pedicularis cap./sud.
	Rhodiolia integrifol.	*Petasites frigidus
	**Sagina Linnaei	*Polemonium acutiflor.
	Saxifraga tricuspid.	*Pyrola spp.
	**Senecio spp.	Rumex arcticus
	*Veronica Wormskjoldii	Senecio triangularis

	Viola epipsila	*Senecio yukonensis*
		Solidago multiradiata
		***Stellaria mon./long.*
		Taraxacum sp.
		Valeriana capitata
		*forb sp.1
		forb sp.3
graminoids		
Calamagrostis spp.	***Agrostis scabra*	***Carex aquatilis*
	Carex aurea	*Carex* spp.
	Juncus spp.	*grass spp.
	Poa spp.	***Luzula parviflora*
	***Trisetum spicatum*	
lichens		
Cetraria cucullata	*Alectoria ochroleuca*	*Cetraria islandica*
Cetraria ericetorum	*Cetraria comm./hep.*	*Dactylina arctica*
Cetraria nivalis	*Cetraria nigricans*	*Peltigera aphthosa*
Cetraria pinastri	*Cladina mitis*	*Peltigera malacea*
Cetraria richardsonii	***Cladonia cariosa*	*Peltigera rufescens*
Cetraria sp.	*Cladonia cenotea*	*Peltigera* sp.
Cladina arbuscula	***Cladonia cervicornal.*	*Thamnolina* sp.
***Cladina rangiferina*	*Cladonia macrophylla*	
***Cladina stellaris*	*Cladonia pocillum*	
Cladonia amaurocraea	***Cladonia* cup	
Cladonia cocc./bell.	*Cladonia* sp.3	
Cladonia crispata	***Pannaria pezizoides*	
***Cladonia sulphurina*	*Peltigera canina*	
Cladonia uncialis	*Peltigera venosa*	
Cladonia tapered	***Psoroma hypnorum*	
Cladonia sp.4	*Solorina crocea*	
Nephroma arcticum	***Stereocaulon* spp.	
Parmelia sp.	*Umbilicaria* spp.	
***Parmeliop. hyperopta*	**crustose	
Peltigera polydactyla		

bryophytes		
**Dicranum* spp.	*Buxbaumia aphylla*	**Aulacomnium palustre*
**Pleurozium schreberi*	**Drepanocladus* sp.1	*Climacium dendroides*
**Polytrichum com./jun.*	***Polytrichum piliferum*	***Drepanocladus* sp.2
**Polytrichum strictum*	***Rhacomitrum canescens*	**Hylocomnium splendens*
**Sphagnum* spp.	**acrocarpic moss	*Leptobryum pyriforme*
		***Rhizomnium* spp.
		**Tomenthypnum nitens*
		***pleurocarpic* spp.
		*liverwort
other plants		
**Equisetum scirpoides*	*Lycopodium alp./comm.*	***Equisetum arvense*
	Lycopodium selago	**Equisetum sylvaticum*
	**algae	*Lycopodium ann./clav.*

Table II-11. Species not present in sites in borrow pits, and with >1% average cover or >10% frequency in undisturbed areas or linear disturbances. Some species are grouped together into genera or other taxonomic groups. Species abbreviations are listed in Appendix 5.

woody plants	**Arctostaphylos rubra*
	**Salix arb. x plan.*
	Salix lanata
forbs	*forb sp.1
lichens	**Nephroma arcticum*
bryophytes	*Rhizomnium* spp.
	**Sphagnum* spp.
	**Tomenthypnum nitens*
other plants	**Equisetum scirpoides*

* species with >1% average cover or >10% frequency in undisturbed sites.

Table II-12. Comparison of selected results from 1978 and 1993, 33 and 48 growing seasons following abandonment of the CANOL pipeline (12a and b). The 1978 data are from Kershaw (1983, 1984). Data for the disturbed sites in 1978 are 'control-corrected'; the + or - values are the mean of the difference (increase or decrease) from the control samples (Kershaw 1983). For the species data, + or - indicate significantly different cover values (at least 2% higher or lower on the disturbance) between the control and disturbance (Kershaw 1984). Average cover values are given for the control sites in 1978. The results from the present study (12b) are actual values, except for the species data in which + or - indicate higher or lower average cover values on the disturbances. This information is only given on disturbances where differences were significant in 1978. Data are sometimes given for western sites only (in brackets) since these were most similar to the 1978 sites (Kershaw pers. comm.). Only species considered common in 1993 and with significant results in 1978 are considered. Noteworthy results are highlighted.

Table II-12a.

	control	pit	access	bladed	track
# sites sampled	14	16	1	8	5
bare ground (%)	8	+60	+20	+44	+18
# plant species	178*	-6	-26	-5	+1
Betula glandulosa	16.3	-	-	-	-
Salix reticulata	0.8	-			
Antennaria spp.	0.5		+		
Artemisia arctica	5.3	-			-
Deschampsia caespitosa	0.5			+	
Carex aquatilis				+	
Festuca altaica	2.1		+	+	
Cetraria islandica	0.9		+	-	
Cetraria nivalis	2.6	-	-	-	-
Cladina arbuscula	4.1	-			
Cladina rangiferina	4.2	-	-	-	
Cladina stellaris	25.8	-	-	-	-
Cladonia gracilis	1.6		-		
Cladonia macrophylla				-	
Pannaria pezizoides		+			
Psoroma hypnorum		+			
Solorina crocea	0.1		+		
Stereocaulon saxatile				+	
Stereocaulon paschale	2.7	-	-	-	-
crustose lichens				+	
soil lichens	0.6	+		+	
Aulacomnium palustre	8.0	-			
Polytrichum commune	10.6	-	+	-	-
Polytrichum juniperinum	1.0	-	-	-	
Polytrichum piliferum		+	+	+	
Polytrichum strictum	0.3				+

* total # species

Table II-12b.

	undist.	pit	access	bladed	track*
# sites sampled**	17	14(6)	3	3	9(4)
bare ground (%)[a]	1	47(75)	9	8	6(10)
# plant species per site	37	45(32)	52	61	52(51)
# species per quadrat	17	12(8)	15	17	16(14)
Betula glandulosa	27.0	-	-	-	-
Salix reticulata	3.7	-			
Antennaria spp.	0.1		-		
Artemisia arctica	0.1	+			+
Carex aquatilis	0.1			+	
grass spp.[b]	1.1		+	+	
Cetraria islandica	0.3		-	-	
Cetraria nivalis	0.7	-	-	-	-
Cladina arbuscula	1.7	-			
Cladina rangiferina	5.2	-	-	-	
Cladina stellaris	15.4	-	-	-	-
Cladonia macrophylla	0.1			-	
Cladonia tapered	1.9		-		
Pannaria pezizoides	0.0	+			
Psoroma hypnorum	0.0	+			
Solorina crocea	0.1		+		
Stereocaulon spp.	2.3	+	+	+	+
crustose lichens	1.1	+		+	
Aulacomnium palustre	5.1	-			
Polytrichum com./jun.	11.1	-	+	-	-(+)
Polytrichum piliferum	0.0	+	+	+	
Polytrichum strictum	6.4				-

* include multi-tracks and heavy-use tracks
** each site contains 15 quadrats
[a] includes cover of bare ground and rock
[b] includes *Festuca altaica* and *Deschampsia caespitosa*

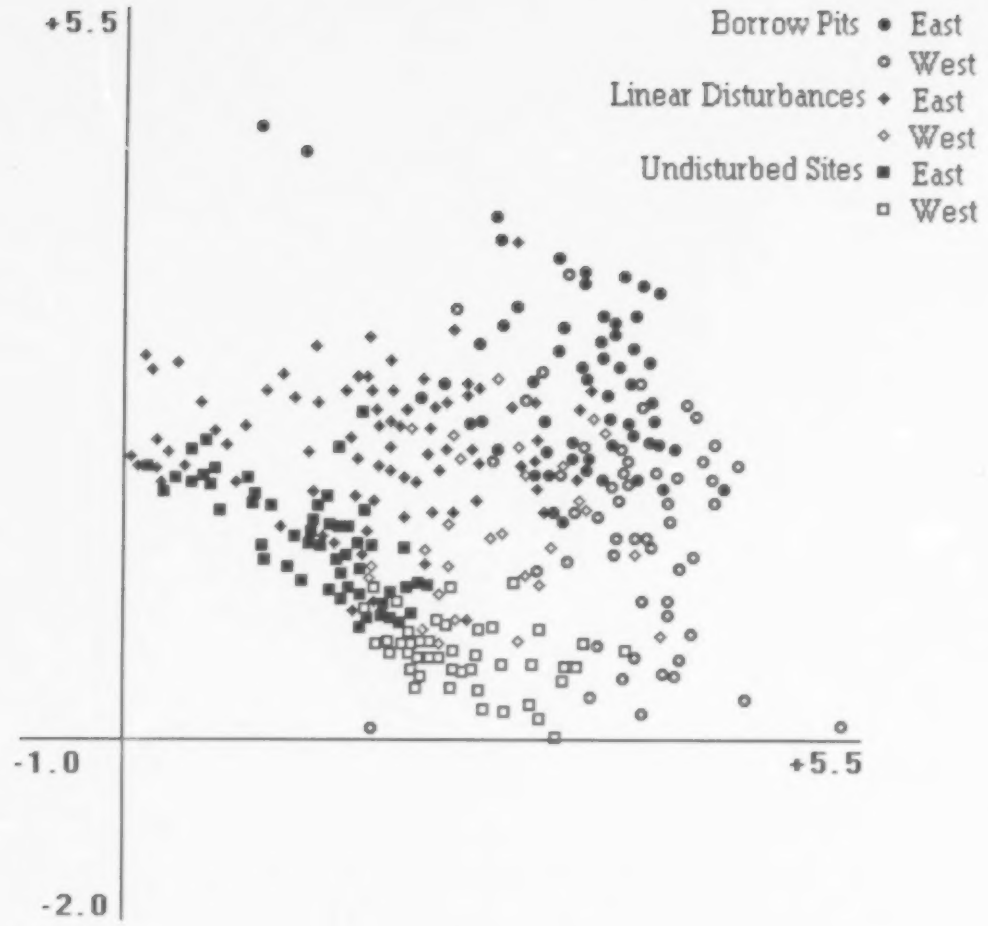

Figure II-1. Scatter plot of samples from eastern and western borrow pits, linear disturbances and undisturbed sites in the DCA ordination. Samples are categorized by region and disturbance type. Approximately 100 of the 460 sample points are not shown for clarity. Axes represent maximum variation in species composition.

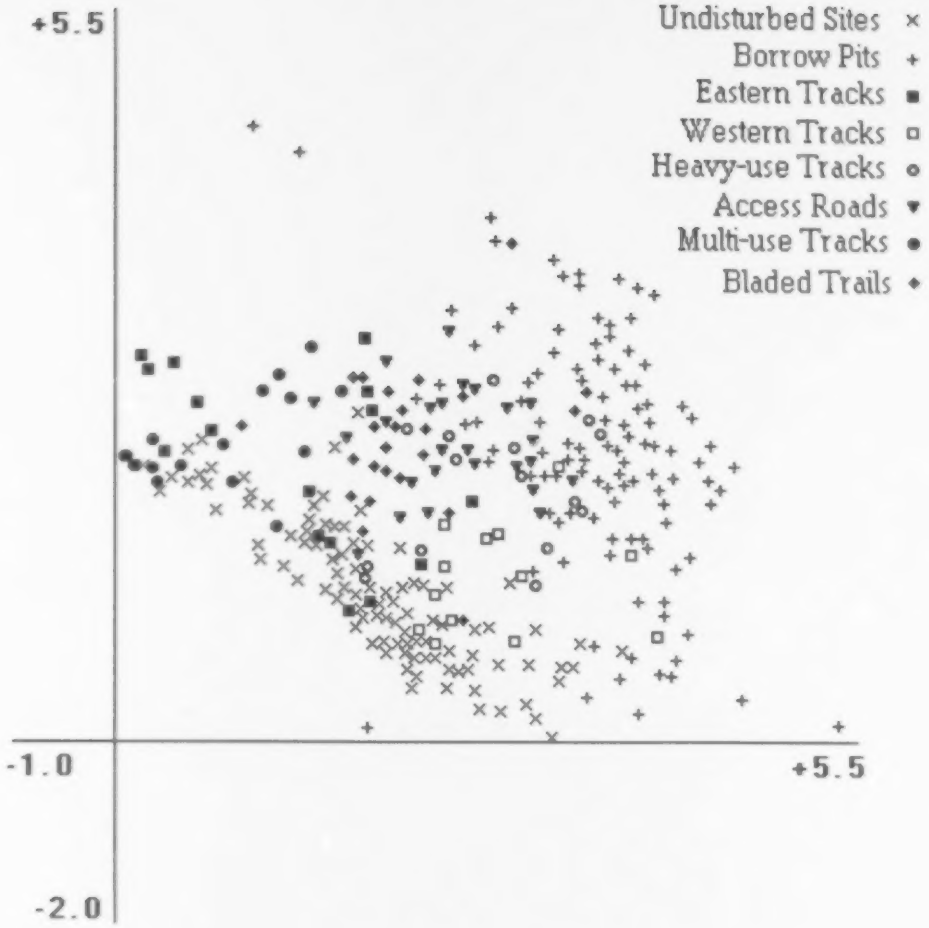

Figure II-2. Scatter plot of samples from borrow pits, different types of linear disturbances and undisturbed sites in the DCA ordination. Samples are categorized by disturbance type, including different categories of linear disturbances. Approximately 100 of the 460 sample points are not shown for clarity. Axes represent maximum variation in species composition. The proximity of sample points from different types of vehicle tracks to borrow pit or undisturbed sample points indicates similarity in species composition.

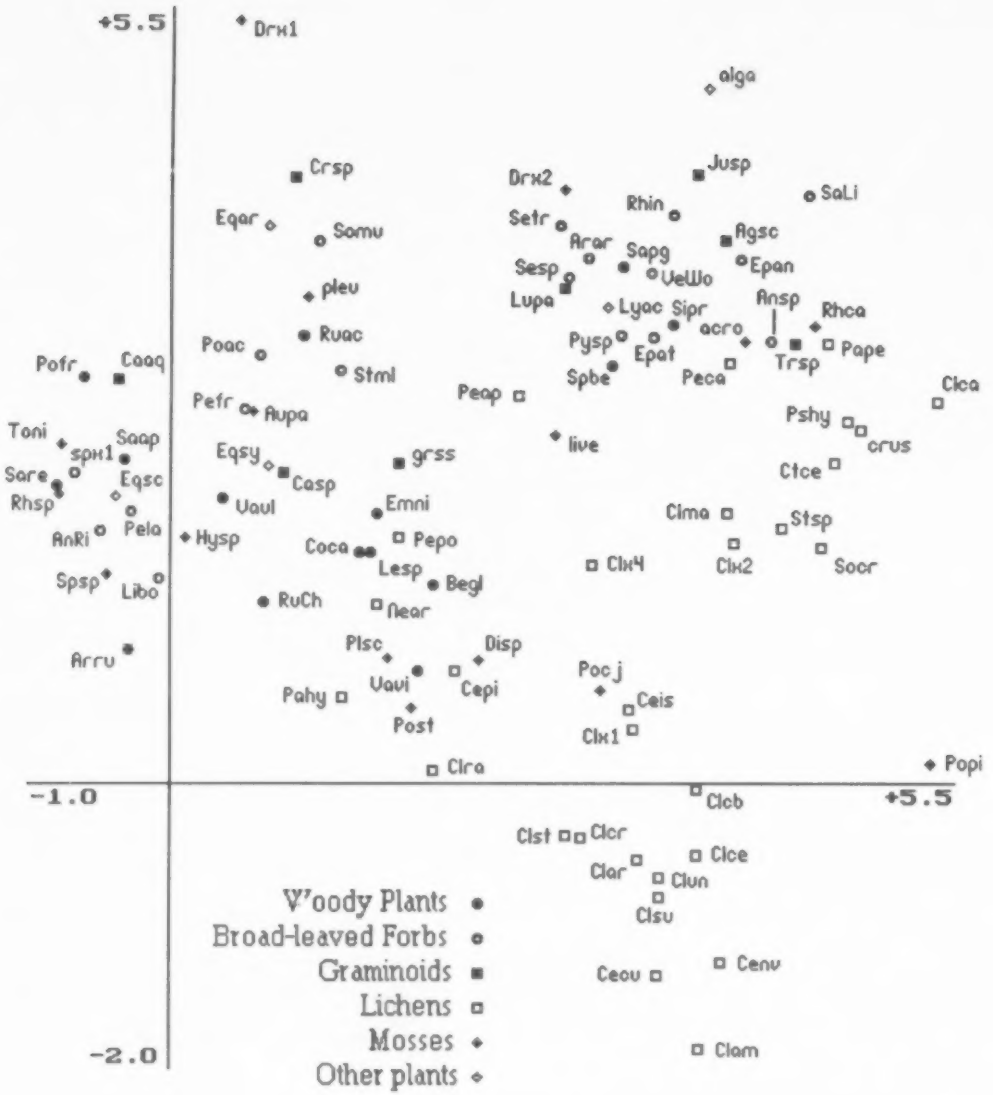

Figure II-3. Scatter plot of plant species in the DCA ordination. Species points are categorized by taxonomic group. Axes represent maximum variation in species composition. Full species names are listed in Appendix 5.

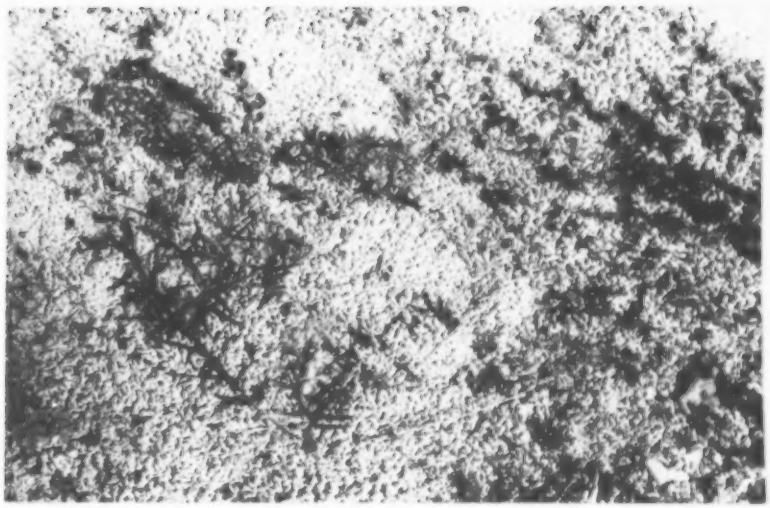

Plate II-1. Plant cover on a borrow pit in 1993. *Epilobium angustifolium* flowers are visible over a mat of *Stereocaulon* spp.

Plate II-2. Lichens in a borrow pit. Several species of *Cladonia* are found on the mineral substrate.

Plate II-3. Vascular plants in a borrow pit. These broad-leaved forbs (*Aster sibiricus* and *Saxifraga tricuspidata*) on a stony surface are uncommon in undisturbed shrub tundra.

Plate II-4. Vegetation in an eastern borrow pit. *Stereocaulon* spp. dominates the surface underneath the beginning of a sparse shrub canopy.

Plate II-5. Vegetation in a western borrow pit. The cover of lichens is very sparse with only a few scattered shrubs.

Plate II-6. Vehicle track in the eastern part of the study area. The prevalence of graminoids is noticeable surrounding the track ruts.

Plate II-7. Heavy-use track in the western part of the study area. Shrubs are scattered over the mineral surface.

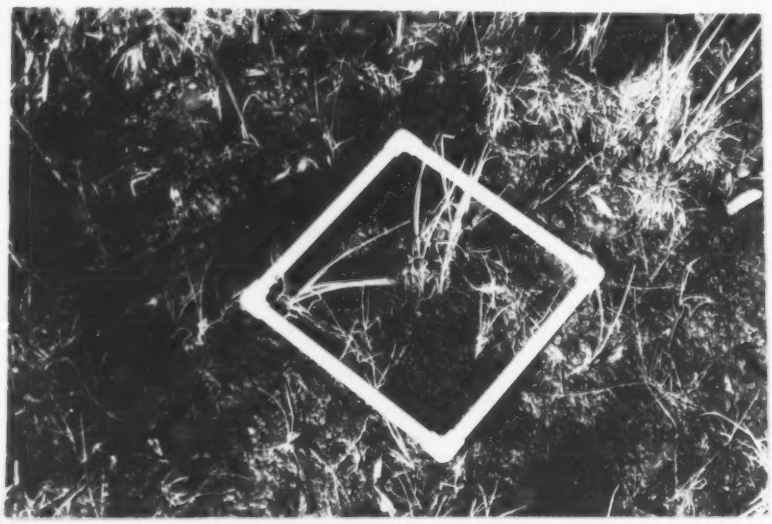

Plate II-8. Moss and *Carex* spp. on a bladed trail. A different plant species composition characterizes this waterlogged linear disturbance site.

Plate II-9. Multi-track disturbance. A track rut is visible, although the disturbed area is more easily identified by the abundant grass.

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III. ABIOTIC FACTORS

Introduction

The removal or maintenance of the organic layer is one of the key factors in the intensity of disturbance (Kershaw 1983a; Ebersole 1985). Mechanical disturbance has three principal effects on the organic layer: removal of organic material, compaction of the organic layer, and accumulation of bladed organic material. The organic layer provides insulation, retains water, and is also a source of seeds and nutrients for plant growth. Typically, a 10-15cm surface organic layer covers wet, clay-rich mineral tundra soils (Tedrow and Cantlon 1958; Haag and Bliss 1974).

Blading trails can completely remove the organic layer to expose mineral soil (Haag and Bliss 1974; Everett 1978; Kershaw 1983a). Other types of vehicle tracks can break and damage the organic mat in several places, particularly with repeated passes (Everett 1978; Ebersole and Webber 1983; Ebersole 1985). Although tracked vehicles and winter roads usually do not remove the peat layer (Hernandez 1973), their impact can compress the surface organic layer (Haag and Bliss 1974; Everett 1978; Kershaw 1983b; Ebersole 1985). An accumulation of soil organic matter can be found on bulldozed slopes and mounds of bladed material (windrows) on the sides of bladed trails (Lawson *et al.* 1978; Ebersole and Webber 1983; Kershaw 1983b).

During primary succession in tundra ecosystems, soil organic matter accumulates slowly under wet, cold, anaerobic conditions (Tedrow and Cantlon 1958; Viereck 1966; Everett 1978). Anthropogenic disturbances generally result in a decrease in organic matter (e.g. Kershaw 1983a, b; Johnson 1987), although increases have been reported (e.g. Herbein and Neal 1990; Forbes 1993).

The removal of the organic layer or a decrease in soil organic matter has been linked to soil warming observed on many disturbed sites (Haag and Bliss 1974; Ebersole and Webber 1983; Kershaw 1983b; Truett and Kertell 1992). Soil temperature is increased by higher thermal conductivity due to compaction of the organic layer or exposure of mineral soil (Haag and Bliss 1974).

Damage or destruction of the organic layer can improve drainage of water-logged soils (Ebersole and Webber 1983; Johnson 1987). Moisture loss can also be rapid on exposed mineral substrates with little organic matter (Haag and Bliss 1974; Gartner *et al.* 1983; Johnson 1987). Moisture retention increases with the accumulation of organic matter (Cargill and Chapin 1987; Borgegard 1990; Heal *et al.* 1981). Soil warming and lower moisture on disturbed sites can increase decomposition of soil organic matter (Ebersole and Webber 1983).

Compaction of the organic layer can lead to an increase in soil moisture (Everett 1978). At some sites, water can

pool in tracks, bulldozed areas and gravel pits (Wein and Bliss 1974; Ebersole and Webber 1983; Kershaw 1983a; Truett and Kertell 1992).

Increases in silt and clay with soil development during primary succession (Viereck 1966) are also important for moisture retention. Fine particles retain moisture (Kershaw 1983a, b), while coarse soil on gravel surfaces can cause rapid moisture loss (Cargill and Chapin 1987; Bishop and Chapin 1989b).

Soil organic matter, moisture, temperature, particle size composition and pH were investigated on borrow pits, linear disturbances and undisturbed sites. Differences in these soil factors among disturbance types were emphasized to explain observed differences in species composition on disturbed sites (Chapter II).

Methods

Microclimate

Two intensive microclimate stations, each with two pit sites (edge and centre), two linear disturbance sites and an undisturbed site, were established to collect a continuous record of soil temperature (see Introduction - Methods; Plates I-9 and I-10). Thermocouples were placed at 5cm depth next to three random vegetation quadrats at each site. Two thermocouples were moved at the Track site at the east station on 30 July so that all locations were within the track ruts. From 29 June to 11 August, 1993, a data logger kept a continuous record of the average soil temperature from the three sensors at each site. The output consisted of hourly and daily averages for each site, as well as daily maximum and minimum temperatures. Daily temperature range was calculated as the difference between the maximum and minimum temperatures for each day.

Soils

Soil pits were dug to the depth of the rooting zone next to three randomly located vegetation quadrats within each site. At one borrow pit site, only two soil pits were dug, since the third was located in another research site. Two additional pits were dug at two linear disturbance sites in order to sample the soil within the track ruts. Each soil profile was described, noting depths and pH (using pH paper) for each layer. The depth of the rooting zone was also recorded. Soil samples collected from each soil horizon within the rooting zone at each pit were double bagged and frozen for lab analysis.

Lab analyses, modified from Kalra and Maynard (1991), included determination of moisture and organic matter content, and particle size analysis. After oven-drying the thawed samples at 30°C constant weight, moisture content was calculated as the percentage of water per dry weight of the

<2mm soil portion. Organic matter was determined by loss on ignition after burning for four hours at 550°C. Hygroscopic water content was evaluated by oven-drying samples at 105°C overnight. Organic matter and hygroscopic water contents were expressed as a percentage of 105°C dry weight of the <2mm soil portion.

After sieving for gravel content (>2mm, expressed as percentage of dry weight), further particle size composition was determined using the hydrometer method (Kalra and Maynard 1991). Within each site, samples were combined to form composite samples of each horizon. The divisions between the sand, silt and clay portions were 0.05mm and 0.002mm; results were expressed as percentages of the <2mm portion. Particle size analysis was only done on a portion of the samples for the tephra layers to characterize this relatively homogeneous soil horizon. Average values of the samples in the tephra layer were then used for subsequent analyses. Average values for all samples were used for organic samples.

Detrended correspondence analysis (DCA) was performed on the following soil characteristics using the CANOCO program (Ter Braak 1988): pH, moisture, hygroscopic water, organic matter, gravel, sand, silt and clay contents. Soil samples from all layers were included in this analysis. The data were not transformed and detrending was by second order polynomials. A description of DCA is given in the Methods section in the preceding chapter. Plots of the results were produced using CanoDraw LITE (Smilauer 1992), NeoPaint (Riley 1993), PicLab (Crocker 1990) and TerraFirma (Eyton 1994).

Differences in soil characteristics among undisturbed areas, linear disturbances and borrow pits within each layer were tested using univariate nested ANOVAs performed on Systat (Wilkinson 1992). Due to lack of independence among the tested variables, a multivariate nested ANOVA was performed on SPSS (Nie 1993) using all the variables. These analyses tested whether the variation was significantly greater among disturbance types than within disturbance types. Tukey tests, also performed on Systat (Wilkinson 1992), were used to interpret further the source of variation among the three disturbance types. In addition, differences among categories of linear disturbances were analyzed using univariate and multivariate nested ANOVAs. Data were log-transformed prior to analysis except for pH in the mineral layer for the univariate nested ANOVA; pH had equal variances among disturbance types (Cochrans C = 1.000, from SPSS, Nie 1993).

Results

Microclimate

Temperature data collected at the East Station before

25 July were considered unreliable due to thermocouple wires found unearthed, presumably by animals, and were excluded from analysis. Soil temperature at 5cm depth was greatest in the Pit Centre site, followed by the Pit Edge site (Figure III-1). The coldest temperatures were found in the undisturbed area, which also had the smallest variation in temperature. Soil temperature recorded in the Track site increased substantially after thermocouple wires were moved to within track ruts on 30 July. Mean daily average, maximum, minimum and range were calculated only when all thermocouples in the bulldozer track site were located within track ruts, for a total of 11 complete days from 31 July to 10 August.

Only 25 complete days were available for analysis at the West Station because of datalogger problems and removal of a thermocouple wire: 3-19 July, 1-4 and 7-10 August. Throughout the summer, soils were warmest in the borrow pit sites and coldest in undisturbed areas (Figure III1-2). At the beginning of the summer, the access road had warmer soil temperature than the bladed trail. The reversal of this pattern on 11 July is visible on the plot of hourly temperatures.

Mean daily average, maximum and minimum soil temperatures were highest for the Pit Centre sites, followed by Pit Edge sites, and lowest for the Undisturbed sites at both microclimate stations (Table III-1). The mean daily temperature range also followed this pattern for the West Station. At both stations, mean daily average and minimum temperatures, but not maximum or range, were greater in the Bladed sites than the Access or Track sites.

Soils

A maximum of three soil layers identified in each soil pit were classified as 'organic', 'tephra' and 'mineral' (Plates III-1, III-2). In most soil pits, an organic layer of partly decomposed humus mixed with litter was too thin to sample. In others, roots were found exclusively in a rich, dark organic layer. Tephra (volcanic ash) was discontinuous throughout the study area ranging from chunks to a solid layer. At most sites, roots were usually found in the gray-brown clay mineral layer below the organic and tephra horizons (Plate III-3). Often large rocks and water were found in soil pits in the undisturbed areas and linear disturbances; gravel was more often present in borrow pits (Plate III-4).

At some sites, mostly in undisturbed areas, roots did not extend beyond the organic and tephra layers into the mineral layer. In nearly all borrow pits, organic and tephra layers were absent. Borrow pits also had the shallowest rooting zone.

The discontinuous tephra layer was characterized by a high silt-sized particle content of over 60%, very low

gravel content and high moisture (Table III-2). Where this layer was present, primarily in the undisturbed sites and some linear disturbances, its composition was relatively uniform with no significant variation between disturbance types (Appendices 11, 12).

Only pH differed significantly between organic layers on undisturbed sites and linear disturbances. This soil horizon was characterized by very high organic matter, moisture and hygroscopic water contents, and low gravel content.

Differences in soil characteristics of the mineral layer among disturbance types were mostly significant (Table III-3). Soils in borrow pits had significantly less moisture, organic matter and hygroscopic water; and significantly greater sand content and pH than soils in vehicle tracks and undisturbed areas. Despite log-transformation, the variances for several variables remained unequal among disturbance types (Cochrans and Bartlett-Box, SPSS, Nie 1993).

Based on the multivariate nested ANOVA, there were no significant differences in any of the soil characteristics among disturbance types ($p<0.05$). Correlations between organic matter, hygroscopic water and moisture content were all above 0.88; those between gravel, sand, silt and clay were over 0.60.

Differences in soil characteristics among linear disturbance types were generally not significant in the univariate and multivariate ANOVAs (Appendices 12, 14). However, soil composition, particularly gravel, water, organic matter and particle size distribution, varied among the categories of vehicle tracks (Table III-4). Multiple track disturbances were most noteworthy for their organic-rich, moist soils with high pH and a thick organic layer.

In a soil pit next to a bulldozer track rut, four layers were clearly distinct: mineral, tephra, organic and a combined layer on top (Plate III-5). Values for most of the soil characteristics in the combined layer were between those for the other layers (Table III-5).

Regional variation in soil composition was evident between eastern and western sites. The organic layer, present in many eastern undisturbed areas and vehicle tracks, was virtually absent from the western region (Table III-2). Greater gravel and sand contents were accompanied by lower moisture, organic matter, and clay in soils in the western region compared to the eastern region.

Despite a low eigenvalue, the percentage variance in the soil characteristics explained by the first axis in the DCA ordination was high due to a low total variance (Table III-6). An eigenvalue measures the variance or dispersion of the species' distributions along an axis, and therefore reflects its importance (Ter Braak 1987a, b, 1988). Cumulative percentage variances of the species data are the

eigenvalues of the respective axes divided by the sum of all eigenvalues (Ter Braak 1990). The other axes, with very low eigenvalues, do not explain much more variation.

On the ordination diagram, the most visible separation of soil samples is that between the three soil layers along the first axis (Figure III-3). Within the organic and tephra layers, samples from different regions and disturbance types were not readily distinct. There was a slight separation of mineral layer samples from different areas (Figure III-3) and different disturbance types along the first axis (Figure III-4).

Samples surrounding a point representing a particular soil characteristic in the ordination diagram would be expected to have higher values for that abiotic factor (Ter Braak 1983). Sand and gravel are associated more with samples from western sites and from borrow pits (Figure III-3). Likewise, high silt content can be related to tephra samples. Higher contents of organic matter, hygroscopic water and moisture would be expected from organic layer samples. The proximity of the points for moisture, organic matter and hygroscopic water suggest strong correlations between these variables.

Discussion

Fifty years after the construction of the CANOL pipeline, most soil characteristics differ significantly between borrow pits and other disturbance types. Insignificant results from the multivariate analyses indicate that these differences are primarily due to dependencies on other evaluated variables. Organic matter, moisture and hygroscopic water are so highly correlated that their interdependence is stronger than their variation among disturbance types.

It is difficult to determine whether variation in soil characteristics is the result of the original disturbance conditions or later effects during the intervening fifty years. Initial differences in soil composition in newly created borrow pits and vehicle tracks might have been greater (or less) than those observed in 1993. Insight into changes in soil characteristics since the initiation of disturbance was also acquired through comparison with the results from Kershaw (1983a, b) from the same region (see below).

<u>Soil characteristics on different types of disturbance</u>

The removal of the organic layer and other top soil layers from borrow pits in the 1940s had resulted in long-term decreases in moisture and organic matter. The scarcity of vascular plants provided little plant material for the accumulation of organic matter in pits. The lack of organic matter and low levels of fine particles reduced the moisture-holding capacity in the mineral substrate. Greater

proportion of coarse particles, lower moisture content and the absence of vegetation all contributed to increased heat flux and warmer soil temperatures in borrow pits.

Greater soil temperatures on linear disturbances, compared to undisturbed sites, were also caused by the reduction in plant cover. Soils in vehicle tracks were kept colder than those in pits by wetter soils, combined with greater shrub and bryophyte cover. Temperatures on the bladed trail exceeded those on the access road at a time when the emergence of shrub foliage shaded most of the access road; very few shrubs were present on the bladed trail.

The compression of the top soil horizons in vehicle tracks may have also resulted in an increase in temperature. As organic matter is compressed, thermal contact between soil particles is improved, increasing heat flux in the soil. Gersper and Challinor (1975) also observed an increase in temperature associated with an increase in bulk density. The increase in temperature when the thermocouples were moved to within track ruts could have been a function of soil compression or decreased shading.

Soils on vehicle tracks may have recovered to pre-disturbance conditions within fifty years, as suggested by the similarity in soil composition between linear disturbances and undisturbed areas. Particularly on multiple tracks, levels of moisture and organic matter exceeded levels on undisturbed sites. Greater proportions of fine particle sizes and organic matter increased moisture-holding capacity. Alternatively, the partial removal of the organic layer in the 1940s may have left the original mineral layer intact. Other soil characteristics not measured in this study might have differed, such as bulk density and nutrient availability.

An accumulation of bladed material was detectable only in one soil pit dug next to a bulldozer track rut (Plate III-5, Table III-5). Soil had been removed from the track rut, piled up beside the track, and could still be distinguished 50 years later as a combination of the organic, tephra and mineral soil layers.

Comparison to soil development 35 years following abandonment

In 1978, Kershaw (1983a, b) investigated particle size composition, organic matter, moisture and pH in soil pits in various disturbance types along the CANOL corridor. The following comparison of soil characteristics in EDST between 1978 and 1993 elucidates patterns of soil development in the fifty years following disturbance in the CANOL corridor. All data cited in this section from 1978 is from Kershaw (1983a, b). The 1978 results also included many sites east of the study area (see the previous chapter for details). The surface substrate in 1978 was compared with the mineral

layer in 1993 for most disturbance types except for undisturbed areas and bulldozer tracks for which the organic layer was also considered.

In 1978, differences in soil characteristics were evident between access roads, bladed trails, bulldozer tracks and controls (Table III-7). Kershaw noted that substrates did not differ much where there was only limited organic matter in undisturbed areas, or where surface layers were relatively intact. Surface layers were not altered on about half of the linear disturbances in 1993. Limited organic layers in undisturbed areas west of camp could also help explain the insignificance of the differences between soils in linear disturbances and undisturbed areas in 1993.

Relative amounts of organic matter and moisture shifted from lower levels on all disturbances compared to controls in 1978, to higher values on most linear disturbances in 1993. Organic matter content increased slightly in borrow pits during the 15 year period. These increases on both vehicle tracks and borrow pits support Kershaw's hypothesis of a rapid rate of organic matter accumulation with time on all CANOL disturbances. However, since the increase was only slight, the accumulation of organic matter on disturbances does not appear to be accelerating with time, as suggested by Kershaw. Monitoring organic matter content on disturbances over time would provide more insight into soil development on anthropogenic disturbances in the Low Arctic.

From 1978 to 1993, an increase in the proportion of fine particles and in organic matter had resulted in a higher moisture-holding capacity in soils on linear disturbances. Overall, soils on linear disturbances in the CANOL corridor have developed from 1978 to 1993 such that they became virtually indistinguishable from undisturbed soils with respect to the measured characteristics. Soils on borrow pits in 1993 remained dry, warm, with high proportions of sand and gravel, and relatively high pH. Since 1978, there was also a slight accumulation of organic matter, increase in moisture and a reduction in gravel content in CANOL pits.

Comparison of soil characteristics on disturbances to other studies

In the Low Arctic, soil development proceeds slowly on newly exposed mineral surfaces. Studies report only minimal development of organic soil on gravel pits (Cargill and Chapin 1987) and some development of a soil profile on an outwash plain 100 years, but not 25-30 years, following deglaciation (Viereck 1966). At the CANOL site, it may take even longer for the development of an organic layer on the western pits due to the scarcity of vegetation.

Low levels of organic matter have been reported on mineral substrates in soils less than ten years after

disturbance (Cargill and Chapin 1987; Johnson 1987; 1.8%, Bishop and Chapin 1989a; 2.8%, Gartner *et al.* 1983). Higher values on CANOL pits after 50 years (3.3%) provide evidence of accumulation of organic matter with primary succession, although it may be decelerating with time. An increase in organic matter from 4.4% at 25-30 years to 5.0% at 200-300 years following deglaciation (10cm depth, Viereck 1966) also demonstrates a slowing of organic matter accumulation during the initial stages of succession. In the same study, organic matter content increased substantially only with the development of an organic layer in climax tundra (Viereck 1966).

There is more discrepancy between the effects of disturbance on organic matter content in vehicle tracks. One study also reported no significant difference in organic matter between vehicle tracks and the control (Chapin and Shaver 1981). An increase (Herbein and Neal 1990) and a decrease (Kershaw 1983a, b) in organic matter in tracks have also been observed. The type and degree of disturbance, plant community and other site conditions influence the effects of linear disturbances on the amount of soil organic matter.

Soil warming is more commonly observed on all types of disturbance (Haag and Bliss 1974; Chapin and Shaver 1981; Ebersole and Webber 1983; Truett and Kertell 1992). The organic layer in undisturbed tundra soils has a lower thermal diffusivity and conductivity, and higher water content than mineral soil; contributing to thermal insulation in undisturbed soils (Haag and Bliss 1974). The removal of vegetation and darkening of wet soil also lowers the albedo of disturbed surfaces, increasing net radiation (Haag and Bliss 1974).

Increased drainage in soils with coarse particles and little organic matter reduces water levels on many gravel surfaces (Johnson 1987; Kershaw and Kershaw 1987; Bishop and Chapin 1989a, b; Borgegard 1990). Damage to vegetation and the surface organic layer can also improve drainage on linear disturbances (Everett 1978; Lawson *et al.* 1978; Ebersole and Webber 1983). Gersper and Challinor (1975) observed lower moisture associated with higher bulk densities in vehicle tracks, which could also be attributed to higher evaporation from exposure to wind and high temperatures.

CANOL linear disturbances were characterized by higher moisture. An increase in soil moisture with compaction of the organic layer occurred on vehicle tracks in other studies (Everett 1978; Ebersole 1985; Herbein and Neal 1990). Water sometimes pools on surfaces of disturbances (Wein and Bliss 1974; Kershaw 1983a; Truett and Kertell 1992).

High gravel and sand contents characterize primary succession sites where organic material has been removed or

buried (Viereck 1966; Kershaw 1983a; Bishop and Chapin 1989a). Gravel surfaces that lack fine particles retain very little water compared to surfaces with more organic material, clay and silt (Kershaw 1983a, b; Kershaw and Kershaw 1987; Bishop and Chapin 1989b).

Although Gartner *et al.* (1983) found a higher pH on organic substrates compared to mineral ones, organic layer samples were less acidic than mineral ones only on CANOL linear disturbances. Viereck (1966) and Messer (1988) noted a decrease in pH with soil development from mineral to organic substrates. Mineral soils in CANOL borrow pits were less acidic than in undisturbed areas. Higher pH on vehicle tracks was also recorded by Challinor and Gersper (1975), Ebersole and Webber (1983), and Forbes (1993).

Soil development in Low Arctic shrub tundra ecosystems

An initial loss of organic material from CANOL borrow pits was accompanied by increased temperature and drainage, conditions which favour decomposition (Ebersole and Webber 1983; Truett and Kertell 1992) and are unsuitable for the accumulation of organic matter. Cargill and Chapin (1987) have also observed only minimal development of organic soil on xeric disturbed sites such as gravel pits.

On CANOL linear disturbances, with no improvement in drainage and little or no initial loss of organic matter, organic matter accumulated rapidly from 1978 to 1993. Despite higher temperatures, slight compression of the top soil layers on bulldozer tracks increased moisture content, favouring plant productivity over decomposition. Other studies have found that organic matter accumulates in water-saturated soils with slow decomposition rates (Janz 1973; Heal *et al.* 1981).

As vascular plants establish, shading reduces soil temperature and moisture loss. The development of a moss layer will also increase water retention (Viereck 1966). Colder, wetter conditions will eventually lead to greater accumulation of organic matter on gravel pits and vehicle tracks.

The long-term accumulation of soil organic matter increases insulation and moisture (Heal *et al.* 1981; Cargill and Chapin 1987; Borgegard 1990). During soil development, moisture-retention also increases from the build-up of fine particles from weathering. Temperature will decrease with these changes in soil characteristics, insulation from the developing organic layer, and shading from revegetation.

Greater pH values in CANOL borrow pits correspond to a negative correlation of pH with organic matter (Cargill and Chapin 1987). Messer (1988) also found that pH decreases with increasing organic matter and terrain age. Acidity increases from anaerobic decomposition in waterlogged conditions (Heal *et al.* 1981), as with organic matter accumulation on disturbed sites.

Increased decomposition from anthropogenic disturbance releases nutrients that were previously unavailable in the soil organic matter, the major reservoir of nutrients in tundra ecosystems (Dowding *et al.* 1981; Everett *et al.* 1981; Ebersole and Webber 1983). An increase in decomposition rate (due to warmer, drier soil) was accompanied by an increase in nutrient availability at several disturbance sites (Ebersole and Webber 1983; Cargill and Chapin 1987; Truett and Kertell 1992).

When the organic layer is removed, the short-term gain in available nutrients is accompanied by a long-term substantial loss in total nutrients (Webber *et al.* 1980). Gravel surfaces are reported to have only limited supply and availability of nutrients (Gartner 1982; Cargill and Chapin 1987; Johnson 1987; Bishop and Chapin 1989a; Borgegard 1990).

With compaction of the surface organic layer, the gain in available nutrients from soil heating and increased decomposition is not accompanied by a depletion of the nutrient stock. Higher concentrations of available nutrients have been observed in vehicle tracks (Chapin and Shaver 1981; Herbein and Neal 1990). However, on CANOL linear disturbances, increased moisture contents may slow decomposition and immobilize nutrients as a long-term effect of disturbance.

Increased nutrient availability and warmer soil temperatures has resulted in an increase in plant productivity on some disturbed sites (e.g. Challinor and Gersper 1975; Herbein and Neal 1990; Truett and Kertell 1992). In other disturbances where the organic layer is removed, a lack of water content and limited nutrient availability limits plant growth (Wein and Bliss 1974; Bishop and Chapin 1989a; Cargill and Chapin 1987). The integration of plant succession and soil development is pursued in the next chapter.

Conclusions

The absence of a thick organic layer on all borrow pits and some linear disturbances was the most noteworthy difference in soils on CANOL disturbances. Variation in soil characteristics between the organic and mineral layers was much greater than among soil samples from different disturbance types. The organic layer contained very high levels of organic matter which retains moisture.

Soils in borrow pits were significantly warmer, drier and less acidic, with less organic matter and greater sand content. Soil characteristics on linear disturbances were not substantially different from those in undisturbed areas, except for warmer soil temperatures.

The accumulation of organic matter on borrow pits and linear disturbances from 1978 to 1993 has been accompanied by an increase in fine particles and water. Particularly on

vehicle tracks, water and organic matter contents have increased to such an extent that in 1993, soil composition on linear disturbances was virtually indistinguishable from undisturbed areas.

Table III-1. Daily average temperature (°Celsius), maximum, minimum and range (maximum - minimum).

Table III-1a. East Station, 31 July to 10 August.

	Pit Centre	Pit Edge	Track	Bladed	Undisturbed
average	12.5	10.9	9.9	10.2	8.1
maximum	15.6	13.1	12.5	12.4	9.4
minimum	10.2	9.0	7.9	8.2	7.0
range	5.4	4.1	4.6	4.2	2.4

Table III-1b. West Station, 3-19 July and 1-4, 7-10 August.

	Pit Centre	Pit Edge	Bladed	Access	Undisturbed
average	12.6	12.0	9.6	9.4	5.9
maximum	16.3	15.4	12.1	12.2	7.9
minimum	9.8	9.2	7.4	7.2	4.1
range	6.5	6.2	4.6	5.1	3.8

Table III-2. Average values of soil characteristics for different disturbance types, subdivided by soil horizon. The number of layers included those where soil samples were not collected. Frequency refers to the percentage of soil pits with that layer within the rooting zone. 'n' is the number of soil pits in which the layer was wide enough for collection. See text (Methods) for complete description of units used for each soil factor. Gravel, water, organic matter, hygroscopic water (hygro. water) and particle sizes are in %. Width and rooting depth are in cm.

	Undisturbed Sites			Borrow Pits			Linear Disturbances		
	East	West	All	East	West	All	East	West	All
rooting depth	14	10	13	4	9	6	11	10	11
number of layers	2.0	1.8	1.9	1.1	1.1	1.1	1.7	1.3	1.6
Mineral									
frequency	0.73	0.95	0.82	1.00	1.00	1.00	0.94	1.00	0.96
n	22	20	42	24	17	41	34	14	48
pH	4.9	5.0	5.0	5.1	5.2	5.1	5.0	5.0	5.0
gravel	24	37	29	24	57	38	18	32	22
water	35	27	32	20	17	19	39	31	37
organic matter	6.8	4.9	6.0	3.9	2.4	3.3	7.6	5.5	7.0
hygro. water	1.7	1.2	1.5	1.1	0.7	0.9	1.8	1.6	1.7
clay	37	26	33	36	17	28	39	33	37
silt	33	26	30	32	20	27	35	37	36
sand	30	47	37	32	63	45	26	30	27
Tephra									
frequency	0.30	0.62	0.43	0	0.06	0.02	0.11	0.21	0.14
n	8	11	19		1	1	4	2	6
width	7	11	9		6	6	4	9	5
pH	4.9	5.1	5.0		5.0	5.0	5.0	5.3	5.1
gravel	1	2	2		1	1	2	1	2
water	66	64	65		52	52	45	69	53

organic matter	8.8	7.7	**8.1**		8.7	8.7	21.2	5.7	**16.0**
hygro. water	1.6	1.4	**1.5**		1.6	1.6	1.6	1.2	**1.5**
clay	20	16	**17**					15	**15**
silt	61	63	**62**					63	**63**
sand	20	21	**21**					22	**22**
Organic									
frequency	0.73	0.10	**0.47**	0	0	**0**	0.56	0.14	**0.44**
n	18		**18**				9	1	**10**
width	13		**13**				15	5	**14**
pH	4.9		**4.9**				5.3	5.0	**5.3**
gravel	5		**5**				1	15	**3**
water	181		**181**				249	83	**233**
organic matter	40.5		**40.5**				46.4	30.9	**44.9**
hygro. water	7.5		**7.5**				10.1	4.9	**9.6**

Table III-3. Summary of results from univariate and multivariate nested analyses of variance (ANOVA) and Tukey multiple comparisons for soil characteristics in the mineral, tephra and organic layers. Only categories significant in either the univariate or multivariate ANOVAs or both are included. The table indicates in which disturbance types the least, moderate and greatest values occur. Categories that were significantly different from one another are indicated by *, ** and ***. The last column indicates the tests (univariate or multivariate) in which the category was significant. All categories are for percent cover except for the number of species. All significance levels are at $p<0.05$ except those in parentheses for the multivariate ANOVA which are at $p<0.10$. Also see Table III-2, Appendices 11, 13, 15.

U = undisturbed
L = linear disturbances
P = borrow pits
u = univariate
m = multivariate

	least	moderate	greatest	sign.
Rooting zone depth	**P	*L	*U	u
Number of layers	*P	**L	***U	u
Mineral layer				
pH	**U	*L	*P	u
Water content	**P	*U	*L	u
Organic matter content	**P	*U	*L	u
Hygroscopic water content	**P	*U	*L	u
Clay content	*P	U	**L	u
Silt content	*P	**U	***L	u, (m)
Sand content	*L	**U	***P	u
Organic layer				
pH	*U	--	**L	u

Table III-4. Average values for soil characteristics for different linear disturbance types, subdivided by soil layer. The number of layers included those where soil samples were not collected. Frequency refers to the percentage of soil pits with that layer within the rooting zone. 'n' is the number of soil pits in which the layer was wide enough for collection. See text (Methods) for complete description of units used for each soil factor. Gravel, water, organic matter, hygroscopic water (hygro. water) and particle sizes are in %. Width and rooting depth are in cm.

	Linear Disturbances						
		East			West		
	Access	Track	Bladed	Multi	Track	Heavy	All
rooting zone depth	9.6	9.5	9.9	20.7	9.1	12.2	11.2
number of layers	1.8	1.3	1.9	2.3	1.5	1.0	1.6
Mineral							
frequency	1.00	1.00	1.00	0.67	1.00	1.00	0.96
n	9	12	9	4	8	6	48
pH	4.9	5.0	4.9	5.2	5.0	4.9	5.0
gravel	33	6	15	37	28	36	22
water	26	52	27	60	29	35	37
organic matter	6.9	9.4	5.3	9.2	4.9	6.4	7.0
hygroscopic water	1.7	2.1	1.4	2.3	1.4	1.7	1.7
clay	35	42	40	36	33	33	37
silt	28	40	39	31	37	37	36
sand	38	18	22	33	31	30	27
Tephra							
frequency	0.11	0.00	0.22	0.17	0.25	0.17	0.14
n	1		2	1	2		6
width	4		6		9		5
pH	4.6		5.2	5.0	5.3		5.1
gravel	7		1	0	1		2
water	55		24	77	69		53
organic matter	10.7		8.1	57.9	5.7		16.0

hygroscopic water	2.0		1.7	1.1	1.2		1.5
clay					15		15
silt					63		63
sand					22		22
Organic							
frequency	0.67	0.25	0.56	1.00	0.13	0.17	0.44
n		3		6	1		10
width		13		16	5		14
pH		5.4		5.3	5.0		5.3
gravel		0		2	15		3
water		274		237	83		233
organic matter		47.4		45.9	30.9		44.9
hygroscopic water		10.5		9.9	4.9		9.6

Table III-5. Soil characteristics for four layers within a soil pit next to a bulldozer track rut.

	Tephra	Organic	Mineral	Combined
depth (cm)	12-19	19-24	24-30+	0-12
pH	5.6	5.0	5.0	4.7
colour	5YR7/1	5Y2.5/1	2.5Y4/4	5Y4/3
gravel (%)	2	15	30	17
water (%)	66	83	22	48
organic matter (%)	5.3	30.9	3.8	8.0
hygroscopic water (%)	1.0	4.9	1.9	2.1
clay (%)	15		37	25
silt (%)	63		37	46
sand (%)	22		26	29

Table III-6. Results from the DCA ordination of soil characteristics. Eigenvalues indicate the dispersion of the species distributions along an axis, and therefore reflect their importance (Ter Braak 1987a, b, 1988). Cumulative percentage variances are the eigenvalues divided by the total variance in the soil characteristics data, also called the total inertia (Ter Braak 1990).

	Axis 1	Axis 2	Axis 3	Axis 4	total inertia
eigenvalues	0.279	0.026	0.017	0.008	0.409
cumulative variance	68.1	74.5	78.6	80.7	

Table III-7. Comparison of selected results from 1978 and 1993, 33 and 48 growing seasons following abandonment of the CANOL pipeline (III-7a and b). The 1978 data are from Kershaw (1983, 1984). Results from 1978 are for the surface substrate in Sombric Brunisol soils. Data were also available for Humic Gleysol soils; however these were very different from undisturbed soils in 1993 and were therefore not reported. The results from 1993 are for the mineral/organic layers except for pits, access roads and bladed trails which only had mineral layers.

Table III-7a.

	control	pit	access	bladed	track
organic matter (%)	70	2	55	5	43
moisture content (%)	215	8	9	10	80
gravel (%)	3	58	90	52	0
sand (%)*	80	88	85	84	65
fine particles (%)	20	12	15	11	35
pH**	4.8	6.3	7.6	4.4	4.4

*sand and fine particles separated with mesh size 0.074mm
**determined using a combination electrode

Table III-7b.

	undisturbed	pit	access	bladed	track
organic content (%)	6/40	3	7	5	7/45
moisture content (%)	32/181	19	26	27	44/233
gravel (%)	29/5	38	33	15	22/3
sand (%)	37	45	38	22	26
fine particles (%)**	63	55	63	79	74
pH	5.0/4.9	5.1	4.9	4.9	5.0/5.3

* include multi-tracks and heavy-use tracks
** includes silt and clay

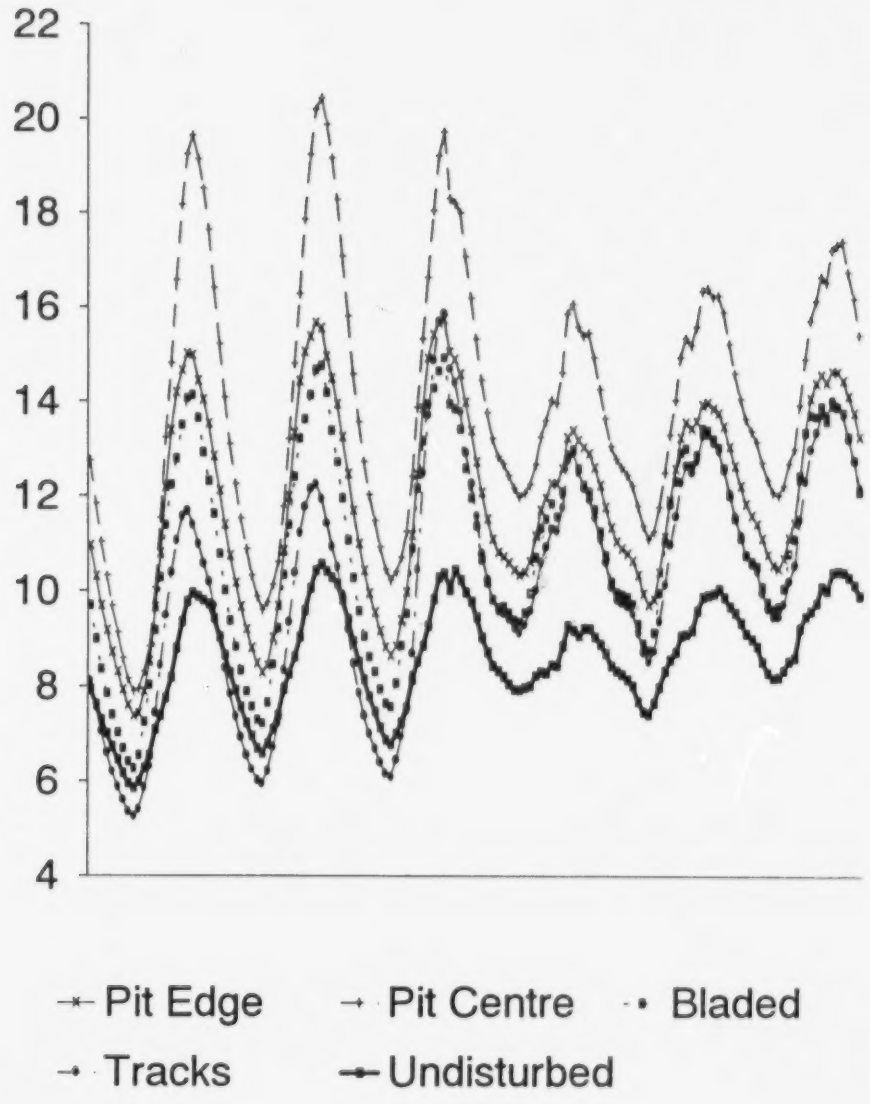

Figure III-1. Hourly average temperatures for sites at the East Station, 28 July to 2 August.

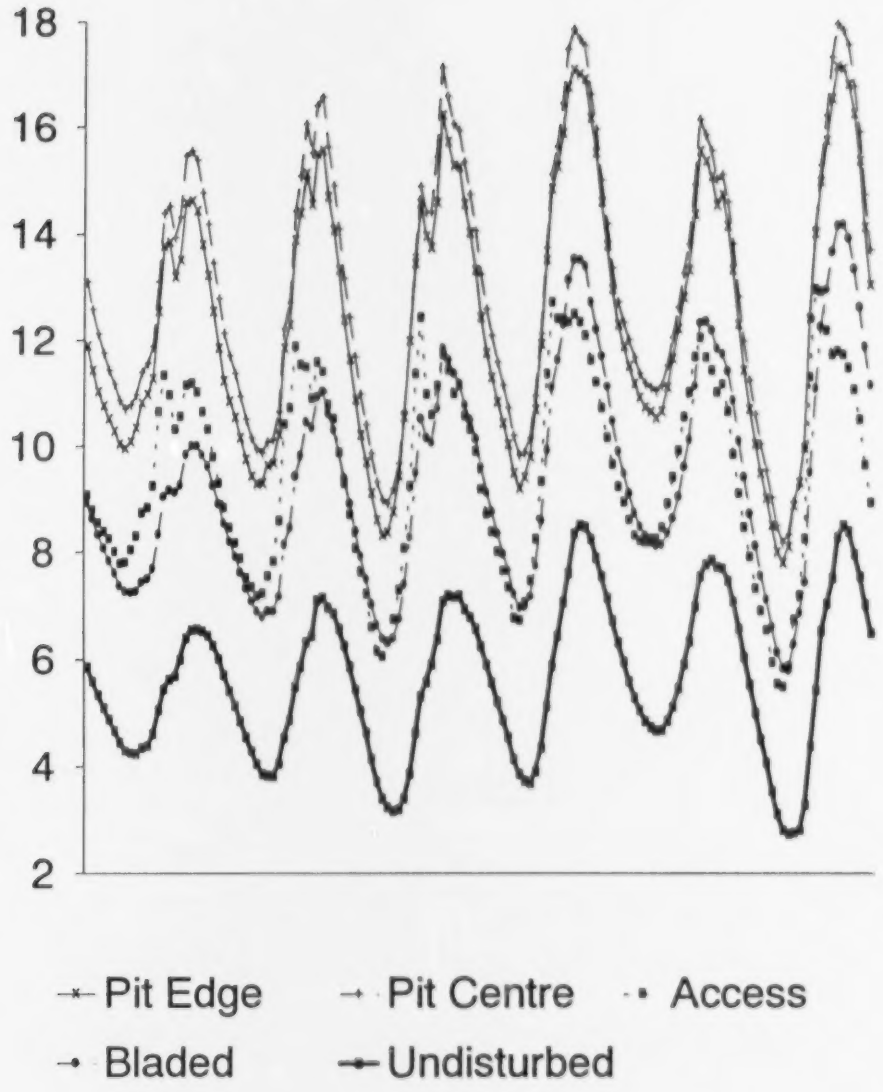

Figure III-2. Hourly average temperatures for sites at the West Station, 9 to 14 July.

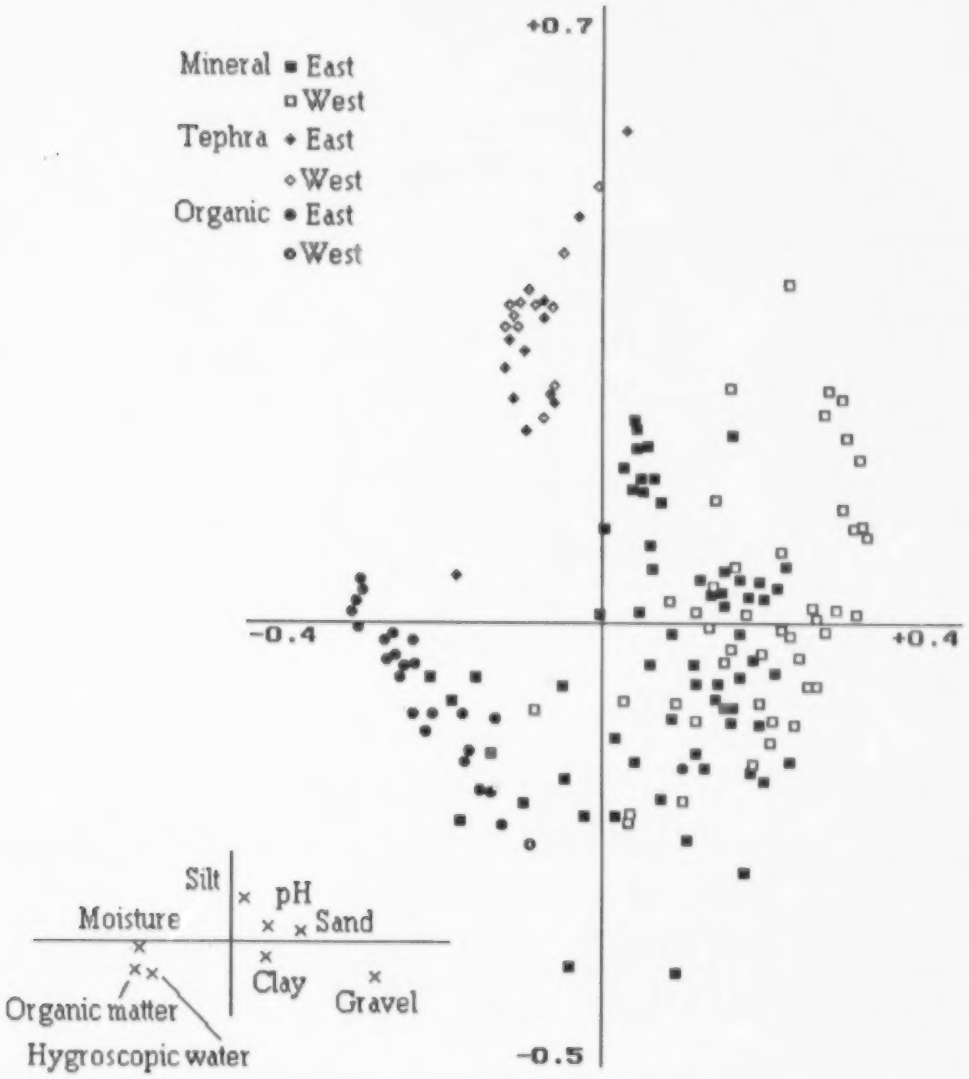

Figure III-3. Scatter plot of soil samples from different soil layers in the DCA ordination. Samples are also categorized by region. Approximately 10 of the 181 sample points are not shown for clarity. These are all samples from the mineral layer located in the right half of the diagram. Axes represent maximum variation in soil characteristics. The scatter plot of soil characteristics below the main ordination diagram is at the same scale.

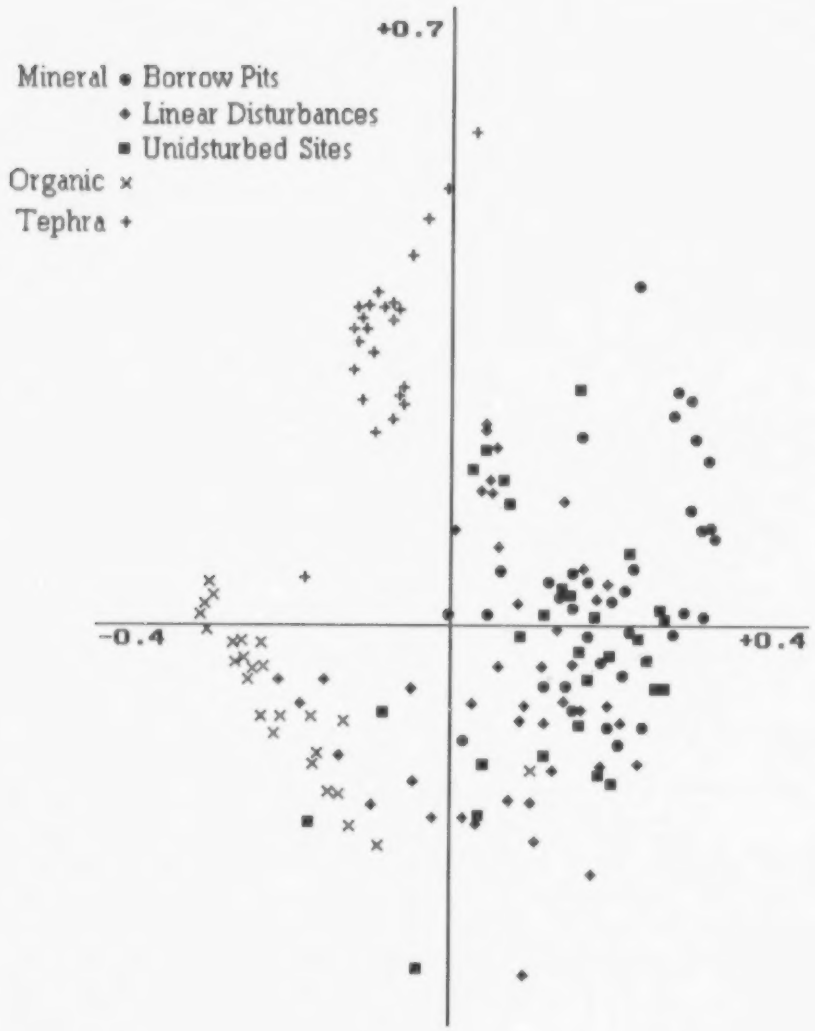

Figure III-4. Scatter plot of soil samples from different disturbance types in the DCA ordination. Samples are also categorized by soil layer. Approximately 10 of the 181 sample points are not shown for clarity. These are all samples from the mineral layer located in the right half of the diagram. Axes represent maximum variation in soil characteristics.

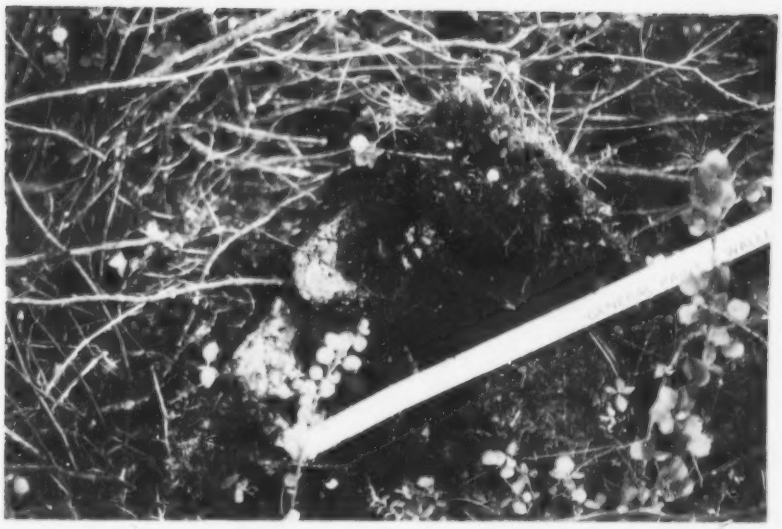

Plate III-1. Organic and tephra layers in undisturbed shrub tundra.

Plate III-2. An organic layer covering the mineral layer in a multi-track disturbance.

Plate III-3. A clay layer underneath a linear disturbance. Note the proximity of the soil pit and the thermocouple wire for relating these factors to species composition in an adjacent quadrat in Chapter IV.

Plate III-4. The mineral layer in western pits, dominated by sand and gravel.

Plate III-5. Soil pit next to a bulldozer track rut. Note the presence of four layers: a mixed layer on top of tephra, organic and mineral layers.

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IV. INTEGRATION OF SPECIES COMPOSITION AND ABIOTIC FACTORS

Introduction

Differences in plant species composition and soil characteristics between borrow pits, vehicle tracks and undisturbed areas were discussed previously. This chapter integrates these results by examining how the differences in the measured abiotic factors explain the variation in species composition on CANOL disturbances.

Previously, studies have related environmental variables to species distributions on anthropogenic disturbances using indirect gradient analysis. Ebersole (1985) plotted isolines for site factors in ordination space. A combination of principal component analysis and stepwise regression analysis was used by Brady (1984) to examine the influence of age, soil factors, slope angle and topographic position on vegetation cover in disturbed sites. More recently, research has taken advantage of newly developed direct gradient analysis techniques, especially canonical correspondence analysis developed by Ter Braak (1986, 1987a).

Canonical correspondence analysis (CCA) is a powerful tool for the interpretation of species composition in relation to the environment. CCA constructs a weighted-averaging ordination in which the ordination axes are constrained to be linear combinations of measured environmental variables (Ter Braak 1986, 1987a; Ter Braak and Prentice 1988). The unimodal species response model used in CCA is appropriate for data sets with wide environmental gradients and community variation (Ter Braak and Prentice 1988). Constrained ordination can be used to determine the importance of measured environmental variables in explaining the variation in species composition. The ordination diagram produced by CCA displays the community variation that is best explained by the set of environmental variables (Ter Braak 1986, 1987a).

Several studies have used CCA as a tool in examining the impacts of disturbance on species composition. Borgegard (1990) studied the effects of surrounding vegetation, age, and the physical and chemical environment on primary succession in abandoned gravel pits. Franklin *et al.* (1993) also used constrained ordination to study succession. Terrain age, soil development and microtopography all had significant roles in the relationship between plant communities and environmental variables on a glacier foreland (Whittaker 1989). The type and degree of disturbance was related to vegetation in China by Xiao-bing (1993); the degree of disturbance was found to be correlated with the primary gradient of variation.

This analytical tool was used to identify the most important environmental factors relating to differences in species composition on the CANOL disturbance sites.

Research focused on two data subsets: samples from all locations with plant species composition and soil characteristics data (the 'entire' data set), and a smaller subset which included only those samples with soil temperature results (the 'microclimate' data set). Using only vegetation quadrats next to soil pits allowed detailed inspection of the relationship between environmental variables and revegetation on specific locations. The proximity of all samples in the microclimate data set isolated the effects of disturbance type from those of topography.

Methods

The entire data set consisted of all sample locations with a soil pit next to a vegetation quadrat, usually three samples per site, for a total of 141 samples (modifications are explained in Chapter III). The microclimate subset included only locations which also had a thermocouple wire next to the quadrat and soil pit (Plate III-3). These 30 samples were from the ten sites at the two microclimate stations described in Chapter III. The three samples from the bulldozer tracks at the East Station included the final thermocouple locations within the track ruts.

The species/samples data sets consisted of species cover estimates for the sample quadrats. Species with low frequency or cover were omitted from the analyses leaving 57 species for the entire data set and 35 for the microclimate data set. Species data were transformed with a logarithmic transformation (log (y+1)) due to the presence of many zeros in the data (as recommended by Ter Braak 1986).

Environmental variables selected for the analysis included: pH, soil moisture, organic matter, hygroscopic water, gravel, sand and clay contents, as well as a measure of the organic layer. The variable for organic layer was given a value of 1 if present and 2 if the layer was thick enough to sample. The microclimate soils/samples data set also included average soil temperature and temperature range from 1-4 and 7-10 August. These were the only days for which comparable temperature data were available for all sites. Average values for soil temperature, sand and clay contents, were applied to all samples within each site. All other data were specific to each sample location. Silt content was not included as an environmental variable since it was dependent on sand and clay contents. Organic matter was omitted from the analysis of the microclimate data set due to a high variance inflation factor which indicates strong correlation with other variables (Ter Braak 1988). Silt and/or organic matter were subsequently added to the ordination diagrams as passive variables which do not affect the ordination results.

Data were used from the soil layer where most of the rooting zone was found, usually the mineral layer. At

several sites where roots were found exclusively in the organic layer, values for sand and clay contents were used from the mineral layer at the same location. Missing values are not allowed in CCA (Ter Braak 1987a, 1988) and particle size analysis could not be performed on the organic layer due to high organic matter content.

Canonical correspondence analysis (CCA) was performed on the species/samples and environmental variables/samples entire and microclimate data sets. In all CCAs, the default scaling was used; species scores were weighted mean sample scores. There was no downweighting of rare species. Despite a slight arch in the ordination diagrams, detrending was not used since it can impose a homogeneous distribution on the data (Ter Braak 1986). The significance of the eigenvalue of the first canonical axis and the trace (the sum of all canonical eigenvalues, Ter Braak 1988) were tested using the Monte Carlo test with 99 unrestricted permutations. All analyses were done using the program CANOCO (Ter Braak 1988). Plots of the results were produced using CanoDraw LITE (Smilauer 1992), NeoPaint (Riley 1993), PicLab (Crocker 1990) and TerraFirma (Eyton 1994).

Additional analyses on the data sets included correspondence analysis (CA) and CCA with a forward selection of variables and significance tests. At each step in the forward selection, the variable that increases the variance explained most is selected (Ter Braak 1990). Further CCAs were performed using only the first few selected variables, a procedure also used by Dale *et al.* (1992) to test the importance of a single environmental variable.

Partial constrained ordination using variables chosen by forward selection helps to select a minimal subset of environmental variables that explain the species composition almost as well as the full set (Ter Braak 1986, 1990; also used by Foster 1992). Partial constrained ordination relates residual variation to other environmental variables after partialling out the effects of covariables (Ter Braak 1986, Ter Braak and Prentice 1988). Partial CCAs were performed using the selected variables as covariables; this was also done by Retuerto and Carballeira (1991), Dale *et al.* (1992) and others to elucidate the importance of one or several variables. This type of analysis tests the significance of the chosen variables in fully accounting for the observed variation in species composition, if the residual variation is insignificant (Palmer 1990; Retuerto and Carballeira 1991). In addition, a partial ordination with all the soil variables as covariables was performed on the entire data set.

The entire data set was further subdivided into separate data sets for borrow pits, linear disturbances and undisturbed areas. CCAs were performed on these data sets to investigate the importance of environmental variables in

different disturbance types. A separate CCA also tested whether different environmental variables were important in the distribution of lichen species.

Results

Only the eigenvalue for the first axis in the CCA of the entire data set was relatively high (Table IV-1). An eigenvalue measures the variance or dispersion of the species distributions accounted for by that axis, and therefore reflects its importance (Ter Braak 1987a, b, 1988). The sum of all canonical eigenvalues measures the variance explained by the selected environmental variables. The species-environment correlation, a measure of the strength of the relation between species and the environmental variables (Ter Braak 1990; Retuerto and Carballeira 1991; Brown *et al.* 1993), had a relatively high value for the first axis only. The first canonical axis and the overall trace were both significant (Monte Carlo permutation, $p < 0.01$).

The eigenvalue for the first axis of the CA ordination (Table IV-2) was considerably higher than that of the CCA ordination. The difference between eigenvalues for the second axis was even greater.

Although correlations between organic matter, moisture and hygroscopic water content were all over 0.9, variance inflation factors remained low enough (<20) for interpretation of the canonical coefficients (Ter Braak 1988). The canonical coefficients are the regression coefficients in the regression that define the ordination axes as linear combinations of environmental variables (Ter Braak 1986, 1988; Ter Braak and Prentice 1988). Absolute coefficients were highest for organic matter, hygroscopic water and moisture on the first two axes (Table IV-3).

Organic matter and both measures of water content in the soil also had absolute t-values well above 2.1. Although t-values are not a measure of significance for canonical coefficients, only environmental variables with t-values over 2.1 are considered to have a unique contribution to the fit of the species data (Ter Braak 1988). All other environmental variables also contributed to the fit of the species data either along the first or second axes, or both.

The inter-set correlations, correlation coefficients between environmental variables and the ordination axes, can also be used to measure the importance of environmental variables in explaining the species data. The other variables are assumed to covary; they are assumed to be constant for determination of canonical coefficients. Unlike canonical coefficients, the inter-set correlations are not unstable when the environmental variables are strongly correlated (Ter Braak 1986). The inter-set correlations were greatest for the presence of an organic layer, organic matter, hygroscopic water, and moisture on

the first axis. Gravel, sand and pH were more strongly correlated with the second axis. These two groups of environmental variables are associated with the primary and residual variations in species composition.

The strengths of the environmental variables on the first two axes are reflected by the ordination diagram (Figure IV-1). Arrows represent the directions of variation in the environmental variables (Ter Braak 1986, 1987a; Ter Braak and Prentice 1988). Longer arrows indicate that those environmental variables are more closely related to the patterns observed in the ordination diagram (Ter Braak 1986, 1987a). In the diagram there is a clear relationship of the organic and water variables with the first axis (and clay to a lesser extent), and of coarse particle sizes and pH with the second axis.

The clearest separation of samples is due to regional variation and the type of soil layer where most roots were found. The projection of sample points onto an arrow yield their values for that environmental variable (Ter Braak 1990). Therefore, the location of sample points in relation to the arrows provides information on soil characteristics of the sites. Samples where roots were found primarily in the organic layer were closely associated with the organic and water variables. Higher values for sand and gravel content were related to samples within the mineral layer. Quadrats located in soils dominated by tephra are also grouped together near the arrow representing silt.

The separation between samples from different disturbance types is not as clear (Figure IV-2). Samples with roots mostly in the organic layer from linear disturbances and undisturbed areas are separated along the second axis. There is also a slight grouping of samples from borrow pits along the second axis. Differences between disturbance types were most closely related to variation in gravel, sand and pH.

Species points are positioned approximately in the centre of the points of sites in which they occur (Ter Braak 1990). The order of species points projected onto the arrows indicates the weighted average position of the species for that environmental variable (Ter Braak 1986, 1987a). The only visible distinction among taxonomic groups in the ordination diagram is the cluster of lichen species (Figure IV-3). These species were closely associated with high gravel and sand in samples where roots were predominantly found in the mineral layer, particularly in borrow pits.

In the CCA with forward selection of environmental variables, the addition of each variable except gravel content was significant ($p<0.05$). No further CCAs or partial CCAs were performed for this data set. In the partial CA with all soil factors as covariables, the eigenvalue for the first axis (Table IV-4) was greater than

the eigenvalue for the CCA ordination. The main gradient of residual variation (partial CA) was greater than the main gradient in variation accounted for by the measured abiotic factors (CCA).

Different environmental variables are important in accounting for the variation in lichen species on disturbed and undisturbed sites. The most prominent variables in the lichen CCA were gravel content and pH (Table IV-5), compared to organic and water variables in the CCA with the entire data set (Table IV-3).

Similarly, canonical coefficients, t-values and inter-set correlations indicate that the importance of environmental variables varied among disturbance types (Table IV-6). Organic matter, the presence of an organic layer and moisture were strongly associated with the variation in species composition on undisturbed sites. The organic layer, moisture and clay were considered the most important variables for the species distribution on linear disturbances. On borrow pits, sand, organic matter and clay had high measures of importance. The eigenvalues for the first axis were 0.328, 0.321 and 0.398 for the pit, linear disturbance and undisturbed data sets with species environment correlations of 0.879, 0.871 and 0.869. The first axis for the pit data set is significant only at $p<0.10$; all other first axes and the trace for all CCAs were significant at $p<0.05$ (Monte Carlo permutations). Organic matter and hygroscopic water were omitted in the linear disturbance and undisturbed data sets respectively since their variance inflation factors were over 20.

Microclimate data set

In the CCA of the microclimate data set, the first two canonical axes with high eigenvalues and species-environment correlations, together explained almost half of the species-environment relations (Table IV-7). The first canonical axis and the overall trace were both significant (Monte Carlo permutation, $p < 0.01$).

Correspondence analysis on the species/sample data set resulted in a slightly higher eigenvalue for the first ordination axis (Table IV-8). The differences between the eigenvalues in the CCA and CA ordinations were greater for the other axes.

Mean soil temperature and clay content were the most important environmental variables for the first and second axes as indicated by their high absolute canonical coefficients, t-values and inter-set correlations (Table IV-9). In the CCA ordination with the forward selection of variables, the additions of average temperature, clay, sand and temperature range were all significant.

With average temperature as the only environmental variable entered into the CCA ordination, the eigenvalue (0.392) and species-environment correlation (0.903) remained

relatively high for the first ordination axis. The eigenvalue for the second unconstrained (residual) axis (0.465) was higher than the first. The eigenvalue for the first residual axis in the CCA with temperature and clay as environmental variables (0.366), was less than that for the first (constrained) axis (0.414).

When temperature was partialled out as a covariable, a partial CCA performed on the remaining environmental variables accounted for only 9.8% of the species variance for the first axis with an eigenvalue of only 0.276. Although the first canonical axis was not significant, the overall trace was significant (Monte Carlo permutation, $p < 0.01$). The remaining variation in the species data after accounting for the both average temperature and clay as covariables in a partial CCA was insignificant ($p < 0.05$).

The importance of both temperature and clay on the first two ordination axes is evident by the length of their arrows in the ordination diagram (Figure IV-4). In contrast to the entire data set, samples from different disturbance types are clearly grouped together in the diagram of the microclimate CCA ordination. The first two axes together separate samples from borrow pits, linear disturbances and undisturbed areas along a diagonal. The separation of samples follows the same direction as the arrows for temperature, organic and water variables. These abiotic factors were related most to the variation in species composition among disturbance types. Clay content is associated more with the variation between samples within the same disturbance type.

Discussion

The similarity in the first eigenvalues from DCA and CCA ordinations is one measure of how well abiotic factors explain species composition (eg. Cramer and Hytteborn 1987; Palmer 1990; Retuerto and Carballeira 1991; Bates 1992). Similar solutions from the two ordinations infer that the dominant gradient in species data is related to the selected environmental variables (Palmer 1986; Ter Braak 1986), and that no important variables have been overlooked (Retuerto and Carballeira 1991). Compared to the above studies, the solutions of the CA and CCA ordinations are similar for the microclimate subset, but not the entire data set.

Soil organic matter, the presence of an organic layer, moisture, hygroscopic water, pH and particle size composition did not explain a substantial portion of the variation in species composition observed on CANOL disturbed and undisturbed sites in EDST. In the partial CA of the entire data set, the residual variation was greater than the variation explained by these soil characteristics. The lack of a relationship between environmental variables and disturbance is also supported by insignificant differences among disturbance types (multivariate nested ANOVA, Chapter

III). Important environmental variables that have been missed may include elevation, topography, parent material and snow depth.

The main gradient of variation in plant species composition in the microclimate data set was accounted for by all the measured soil characteristics. Topographic and climatic factors omitted from the study would have had less influence in this data set due to the proximity and similar topography of the microclimate sites. The difference between the results of the two data sets could also be explained by the inclusion of temperature in the microclimate ordination.

Soil warming from the removal of the vegetative and/or organic layers had the greatest impact on species composition. Average soil temperature alone accounted for a large part of the variation in species composition within the microclimate data set; the residual variation from the other environmental variables was insignificant. The combination of temperature and clay was the smallest subset of the measured environmental variables that best explained the species data.

Soil particle size composition was important in explaining residual variation within disturbance types due to regionality or other factors. Sand and gravel were both related to differences between pits and other disturbance types, and were important abiotic factors in the variation in species composition on borrow pits. Sand content was significantly higher in borrow pits; both sand and gravel varied substantially between eastern and western pits (Chapter III).

Organic matter content and the presence of an organic layer were both strongly related to the distribution of samples and species on all CANOL study sites. However, the organic layer was not an important factor in the microclimate data subset. Its effects might have been overshadowed by temperature, or might not have been as pronounced over a small area. Organic and water variables were most strongly linked to the differences in the soil layer. The variation in these soil characteristics was much greater between the mineral and organic layers than among disturbance types (Chapter III).

The separation of samples based on the soil layer where most roots were found illustrates the importance of the organic layer in revegetation of anthropogenic disturbances. The distribution of samples is not surprising since soil characteristics vary substantially between soil layers (Chapter III). The impact of constraining the ordination axes to be linear combinations of environmental variables is demonstrated by comparing ordinations of only species composition or abiotic factors (Figures II-1 and III-4). The CCA ordination diagram reflects the differences in soil characteristics more than the variation in species

composition.

The difference in species composition among disturbance types, as explained by the measured environmental variables, was related only to the residual variation and not the primary gradient of variation. The residual variation explained by the second axis was considerably less than the main variation, as indicated by low eigenvalues and species-environment correlations. Within the entire data set, regionality and the soil horizon where most roots were found were much more important in explaining the variation in species composition.

The clear grouping of samples in the microclimate CCA diagram demonstrates a strong effect of disturbance type in long-term revegetation within a homogeneous plant community. In borrow pits, the organic layer was completely removed, resulting in a new substrate and different species composition. The impact of vehicle tracks, where the organic layer was only partially removed or compressed, was less severe.

Comparison to other studies

Studies of the relationship between abiotic factors and species composition often do not include temperature (e.g. Hernandez 1973; Bishop and Chapin 1989; Borgegard 1990). Temperature was strongly related to the first and second axes of the only constrained ordinations performed on vehicle track disturbances in the High Arctic (Forbes 1993). On the CANOL sites, soil temperature was strongly related to species composition; different species may be responding to temperature or other related factors. Chapin (1983) suggests that low temperature affects plant growth indirectly through its effects on annual carbon gain, nutrient availability and organic matter mineralization. Soil temperature may also be highly correlated to other factors directly related to plant growth such as length of growing season and date of snow melt (Chapin 1983). Temperature could also be a function of plant composition; shrubs and moss would have a cooling effect on the soil.

Ebersole (1985) found that pH, organic matter and moisture were all correlated with the variation in vegetation on disturbed sites. pH and organic mat depth were both important environmental variables explaining variation in species composition in the High Arctic (Forbes 1993). In the entire CANOL data set, pH was strongly related to the second axis; organic and water variables were important on both axes.

Moisture also contributed a significant role in revegetation of a glacial plain as one of the microtopographic variables (Whittaker 1989). The major environmental factors influencing vegetation development in 2 to 80 year-old mining disturbance sites in sub-Arctic forest were a combination of environmental conditions

(including soil drainage and macropore space), climate and site age (Brady 1984). Changes in particle size composition and drainage patterns can restrict germination on disturbed sites (Kershaw 1984; Bishop and Chapin 1989; Borgegard 1990). Particle size composition, an important abiotic factor within CANOL disturbances, influences both drainage and macropore space.

Lichens were the only taxon that responded as a group to environmental variables (Figure IV-3). Lichen species responded to pH, the proportion of coarse particles and the presence of an organic layer. The distribution of all species corresponded more with the variation in organic matter and moisture. Cox and Larson (1993) also performed separate analyses for bryophytes and vascular plants and found that they responded differently to environmental variables. Forbes (1993) discovered that cryptogams accurately reflected subtle changes in soil pH in the High Arctic.

Ebersole and Webber (1983) observed an increase in the abundance of grasses and willows on mounds of organic soil in northern Alaska. These plants are adapted to the high nutrient turnover rates caused by increased decomposition rate on these well-drained and aerated mounds (Ebersole and Webber 1983). Graminoids dominate warm soils with increased nutrient availability (Truett and Kertell 1992). In these studies, graminoids and willows are associated with conditions of a thick organic layer, high organic matter content and low moisture.

On the CANOL sites, the covers of *Carex* spp. and *Salix* spp. were greatest for multiple track disturbances where mounds of organic material would have been created next to track ruts (Appendix 3). Grass spp., *Carex* spp. and several *Salix* spp. were associated with high organic matter, a thick organic layer, but high moisture content (Figure IV-3). These species were primarily found in linear disturbance sites where the roots were found almost exclusively in the organic layer. Willows and graminoids may be responding to the continual presence of an organic layer, and increased light and temperature due to removal of the shrub layer.

Conclusions

The selected soil characteristics accounted for a substantial portion of the variation in species composition only in the microclimate data set which covered a smaller, more homogeneous area. Soil temperature was strongly related to differences in plant composition on borrow pits, linear disturbances and undisturbed sites.

For the entire data set which covered all CANOL sites, organic matter, the presence of an organic layer, hygroscopic water and moisture contents were all considered important among the measured environmental variables. Most of the variation between samples was due to regionality as

well as different soil horizons within the rooting zone. Particle size and pH explained some of the residual variation and were more closely related to differences among disturbance types.

Table IV-1. Summary of results from the CCA ordination of the entire data set. Eigenvalues and species-environment correlations are explained in the text. Cumulative percentage variances of the species data and the species-environment relations are the eigenvalues divided by the sum of all unconstrained and constrained eigenvalues respectively (Ter Braak 1990).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.355	0.111	0.093	0.052
Species-environment correlations	0.846	0.570	0.583	0.627
Cumulative percentage variance of species data	8.4	11.0	13.2	14.4
Cumulative percentage variance of species-environment relation	48.5	63.6	76.4	83.4
Sum of all unconstrained eigenvalues = total inertia				4.249
Sum of all canonical eigenvalues				0.732

Table IV-2. Summary of results from the CA ordination of the entire data set. Eigenvalues are explained in the text. Cumulative percentage variance of the species data is the eigenvalue for that axis divided by the sum of all eigenvalues (Ter Braak 1990).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.540	0.430	0.285	0.212
Cumulative percentage variance of species data	12.7	22.8	29.6	34.5
Sum of all unconstrained eigenvalues = total inertia				4.249

Table IV-3. Canonical coefficients, corresponding t-values and inter-set correlations for standardized environmental variables on the first two axes of the CCA ordination of the entire data set. Absolute t-values over 2.1, and high absolute coefficients and correlations are underlined.

	canonical coefficients		t-values		inter-set correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
organic matter	**-1.26**	**-1.96**	**-5.14**	**-3.52**	**0.664**	-0.064
hygroscopic water	**0.83**	**1.25**	**3.63**	**2.38**	**0.723**	0.030
moisture	**0.82**	**1.15**	**4.77**	**2.93**	**0.723**	0.010
organic layer	0.46	-0.45	**5.23**	**-2.21**	**0.721**	-0.092
clay content	0.26	0.30	**3.50**	1.77	0.349	-0.118
gravel content	-0.21	0.27	**-2.48**	1.38	-0.450	**0.273**
sand content	0.12	0.54	1.34	**2.55**	-0.206	**0.318**
pH	-0.06	0.42	-0.96	**3.01**	0.062	**0.352**

Table IV-4. Summary of results from the partial CA ordination of the entire data set using all soil factors as covariables. Eigenvalues are explained in the text. Cumulative percentage variance of the species data is the eigenvalue for that axis divided by the sum of all eigenvalues (Ter Braak 1990).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.390	0.242	0.213	0.181
Cumulative percentage variance of species data	11.1	18.0	24.0	29.2
Sum of all unconstrained eigenvalues after fitting covariables				3.517
Sum of all unconstrained eigenvalues = total inertia				4.249

Table IV-5. Canonical coefficients, corresponding t-values and inter-set correlations for standardized environmental variables on the first axis of the CCA with only lichen species. Organic matter was omitted since its variance inflation factor was over 20 (as recommended by Ter Braak 1988). The first axis with an eigenvalue of 0.206 explained 6.2% of the species data and 44.9% of the species environment relation. Absolute t-values over 2.1, and high absolute coefficients and correlations are underlined.

	canonical coefficients	t-values	inter-set correlations
gravel content	**-0.66**	**-3.45**	**-0.287**
pH	**-0.51**	**-3.69**	**-0.301**
sand content	**0.50**	**2.13**	-0.076
organic layer	0.43	**2.51**	**0.394**
clay content	-0.21	-1.03	0.017
moisture	0.16	0.41	**0.391**
hygroscopic water	0.12	0.31	**0.393**

Table IV-6. Canonical coefficients, corresponding t-values and inter-set correlations for standardized environmental variables on the first axis of the CCAs for the three different disturbance types. Absolute t-values over 2.1, and high absolute coefficients and correlations are underlined.

	canonical coefficients	t-values	inter-set correlations
BORROW PITS			
clay content	**1.65**	**6.23**	**0.641**
sand content	**1.23**	**3.66**	**-0.471**
organic matter	**0.83**	**2.53**	**0.447**
hygroscopic water	-0.45	-2.02	0.382
pH	-0.33	**-2.76**	-0.339
moisture	0.24	0.99	0.264
organic layer	-0.08	-0.72	-0.065
gravel content	-0.06	-0.29	**-0.433**
LINEAR DISTURBANCES			
moisture	**0.46**	1.84	**0.665**
clay content	**0.46**	**3.33**	0.430
organic layer	**0.33**	**2.31**	**0.608**
pH	0.25	**2.49**	0.401
sand content	-0.16	-0.95	-0.248
gravel content	-0.04	-0.31	**-0.568**
hygroscopic water	0.01	0.03	**0.636**
UNDISTURBED SITES			
moisture	**1.01**	**4.53**	**0.751**
organic matter	**-0.70**	**-2.86**	**0.673**
organic layer	**0.57**	**3.98**	**0.765**
clay content	0.25	2.08	0.469
sand content	0.24	1.97	-0.090
gravel content	-0.17	-1.27	-0.324
pH	-0.04	-0.37	0.041

Table IV-7. Summary of results from the microclimate CCA ordination. Eigenvalues and species-environment correlations are explained in the text. Cumulative percentage variances of the species data and the species-environment relations are the eigenvalues divided by the sum of all unconstrained and constrained eigenvalues respectively (Ter Braak 1990).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.431	0.249	0.203	0.183
Species-environment correlations	0.923	0.812	0.902	0.888
Cumulative percentage variance of species data	13.4	21.1	27.4	33.1
Cumulative percentage variance of species-environment relation	30.2	47.6	61.8	74.6
Sum of all unconstrained eigenvalues = total inertia				3.217
Sum of all canonical eigenvalues				1.426

Table IV-8. Summary of results from the microclimate CA ordination. Eigenvalues are explained in the text. Cumulative percentage variance of the species data is the eigenvalue for that axis divided by the sum of all eigenvalues (Ter Braak 1990).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.532	0.428	0.315	0.292
Cumulative percentage variance of species data	16.6	29.8	39.6	48.7
Sum of all unconstrained eigenvalues = total inertia				3.217

Table IV-9. Canonical coefficients, corresponding t-values and inter-set correlations for standardized environmental variables on the first two axes of the microclimate CCA ordination. Absolute t-values over 2.1, and high absolute coefficients and correlations are underlined.

	canonical coefficients		t-values		inter-set correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
mean temperature	**0.49**	**-0.86**	**2.19**	**2.22**	**0.836**	-0.299
clay content	**-0.42**	**-0.75**	**-3.67**	**-3.81**	**-0.634**	**-0.487**
organic layer	-0.27	-0.36	-1.63	-1.27	-0.439	-0.027
temperature range	0.24	0.16	1.14	0.45	**0.757**	-0.239
gravel content	-0.19	-0.12	-1.07	-0.39	0.301	0.090
sand content	0.11	0.36	0.61	1.18	0.381	0.170
hygroscopic water	0.10	0.16	0.53	0.48	-0.441	0.096
moisture	-0.01	0.14	-0.11	0.61	-0.339	0.234
pH	0.00	-0.37	0.01	**-2.18**	0.066	-0.386

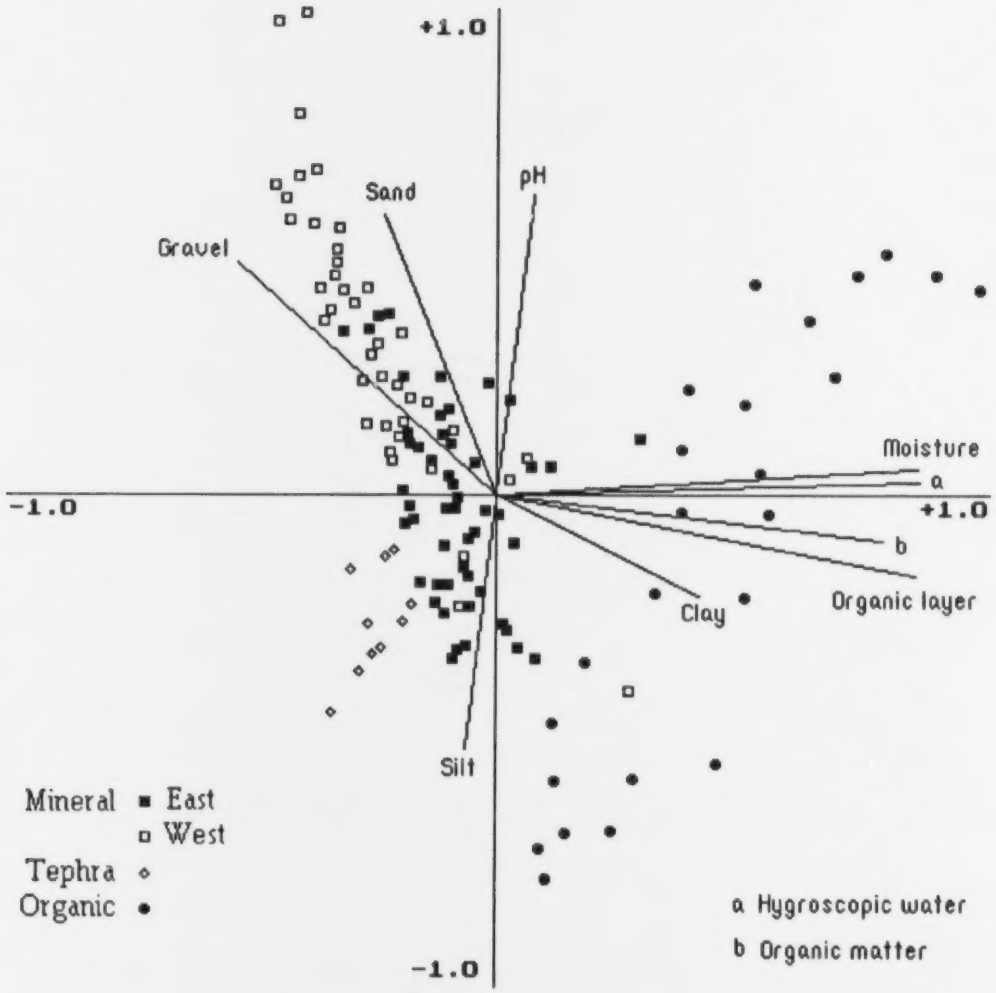

Figure IV-1. Biplot of samples and environmental variables in the CCA ordination of the entire data set, categorized by soil layer and region. Approximately 5 of sample points are not shown for clarity. These are located in the upper left corner near the origin. The ordination diagram represents the variation in species composition that is best explained by the environmental variables. Arrows represent the direction of variation in the environmental variables.

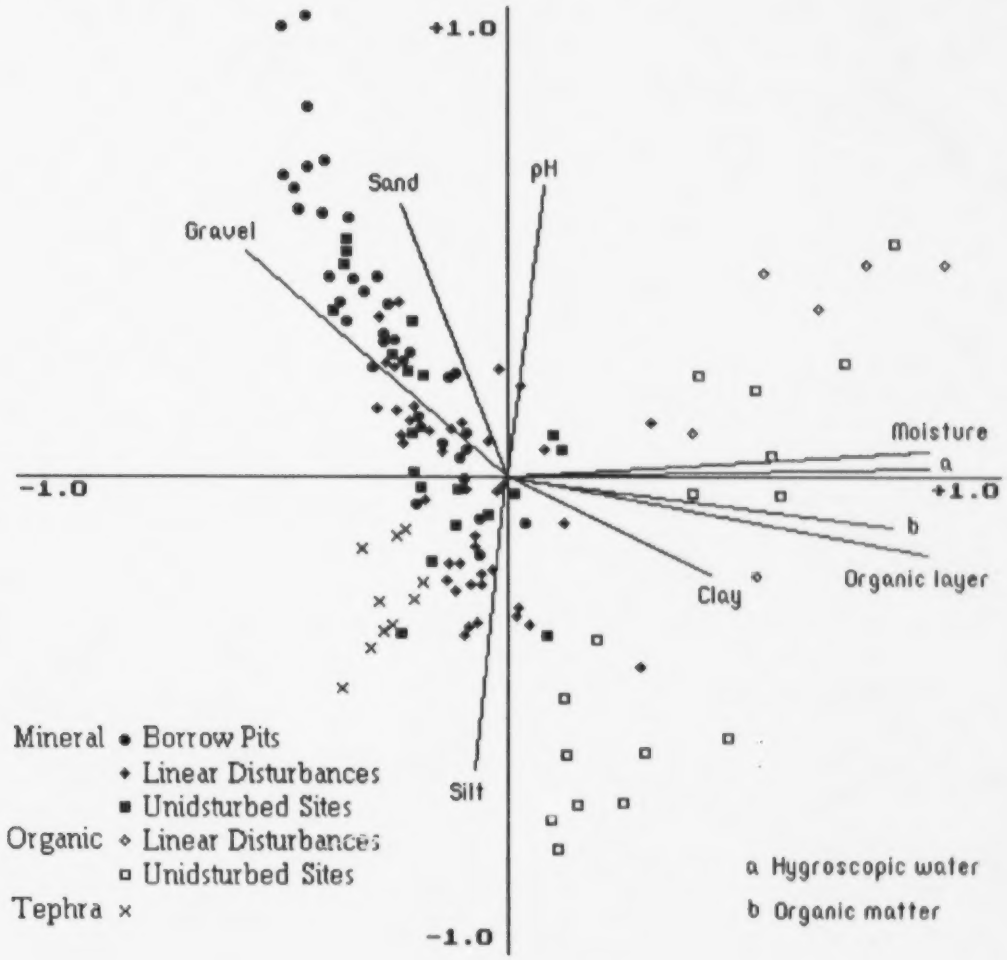

Figure IV-2. Biplot of samples and environmental variables in the CCA ordination of the entire data set, categorized by soil layer and disturbance type. Approximately 5 of sample points are not shown for clarity. These are located in the upper left corner near the origin. The ordination diagram represents the variation in species composition that is best explained by the environmental variables. Arrows represent the direction of variation in the environmental variables.

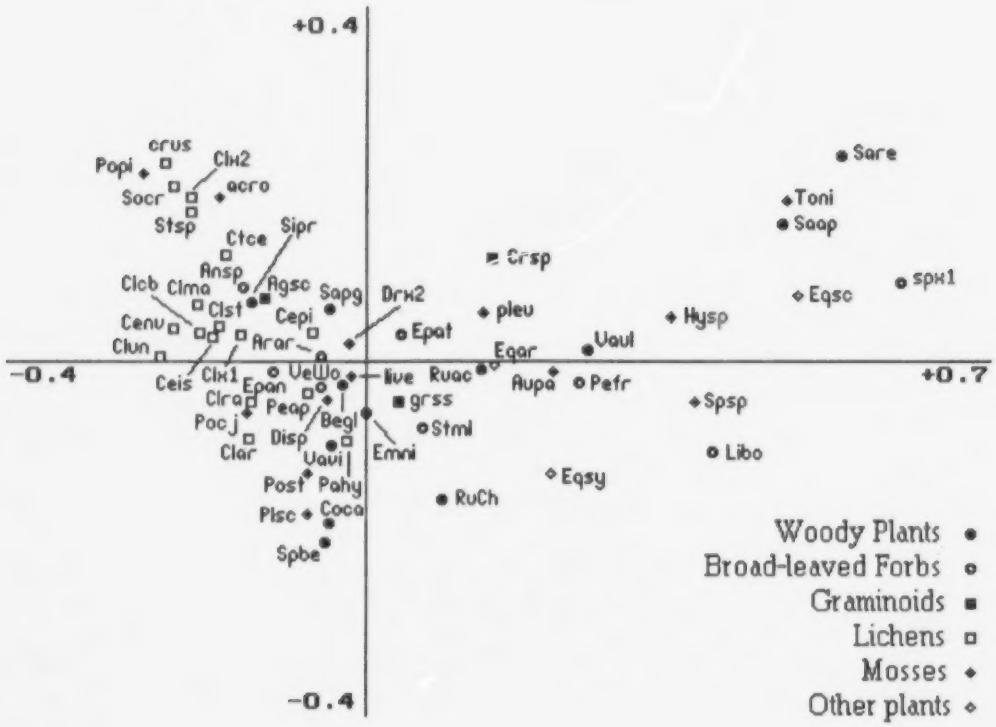

Figure IV-3. Scatter plot of plant species in the CCA ordination of the entire data set. Species are categorized by taxonomic group. The ordination diagram represents the variation in species composition that is best explained by the environmental variables. Species points are the centroids of the samples in which they occur.

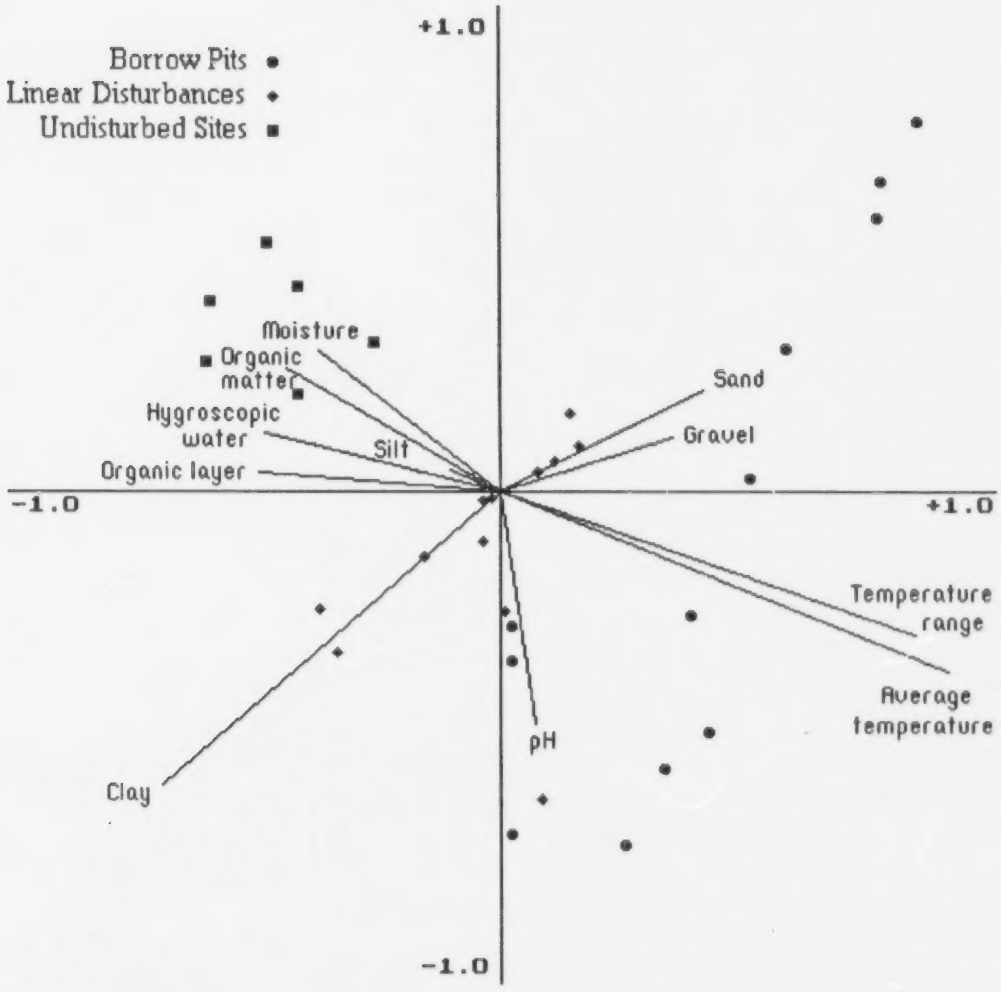

Figure IV-4. Biplot of samples and environmental variables in the CCA ordination of the microclimate data set. Samples are categorized by disturbance type. The ordination diagram represents the variation in species composition that is best explained by the environmental variables. Arrows represent the direction of variation in the environmental variables.

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V. CONCLUSIONS

Forty-eight years following the abandonment of the CANOL pipeline, the long-term effects of anthropogenic disturbance are still evident through significant and substantial differences in plant species composition and soil characteristics among borrow pits, linear disturbances and undisturbed areas. Regional variation in the Erect Deciduous Shrub Tundra plant community, although prominent, did not override the variation among disturbance types except when plant composition and abiotic factors were integrated. More specific conclusions include (numbers refer to the 4 objectives listed in the Introduction):

1. Disturbance sites were characterized by lower abundance of woody plants and overall greater species richness than undisturbed areas. Borrow pits were still dominated by pioneer species in the preliminary stages of succession. Pioneer species persisted on linear disturbances in the intermediate succession stages, although some species replacement was evident.
2. The organic layer with high organic matter and moisture contents was found mostly in undisturbed areas and some linear disturbances. In borrow pits, the mineral layer was warmer, drier, less acidic, and contained less organic matter and fine particles than the mineral layer in undisturbed areas. Soils in vehicle tracks were virtually indistinguishable from undisturbed soils except for higher temperatures.
3. Within a relatively homogeneous plant community, soil temperature was the most important measured environmental variable related to the difference in species composition among disturbance types. The selected soil characteristics did not account for a substantial portion of the variation among disturbance types within the entire study area. The organic and water variables were most important in explaining differences in species composition. pH and coarse particle sizes accounted for some of the residual variation which was more directly related to the differences among disturbance types.
4. Differences in methodology precluded direct comparisons of species composition between 1978 and 1993 in the CANOL corridor; conclusions remain inferential at best. Total plant cover, species richness, organic matter content, the proportion of fine particles, and water all notably increased. Despite apparent similarities in species composition, changes in the relative abundance of a few species on disturbed areas

between 1978 and 1993 indicated their affinity for particular stages in successional development.

Management Implications

The effects of unregulated construction on the soils and plant communities in the CANOL corridor are both visible and significant almost half a century later. Plant succession and soil development proceed very slowly, particularly in primary succession sites. Construction activities that destroyed the vegetation and soil could remain permanent landmarks for decades and even centuries. Borrow pits and roads that remain unvegetated invite other uses such as hunting and recreation along the CANOL Road.

Secondary succession can progress faster on vehicle tracks. Soils and plant composition on linear disturbances were more similar to undisturbed areas in 1993 than in 1978. There were even some vehicle tracks that could not be located in 1993. However, it may still take many decades for species characteristic of undisturbed shrub tundra to completely replace the more diverse flora typical of disturbances. Even subtle changes in species composition may affect the fauna (see Kershaw 1983).

One of the more notable differences between borrow pits and linear disturbances (primary and secondary succession sites) was the complete absence of the organic and other surface soil layers in pits. Although the variable 'organic layer' may not have been directly related to the variation in species composition among disturbance types, samples were mostly differentiated based on which soil layer dominated the rooting zone. The organic layer influences revegetation directly as a source for seeds and nutrients, and indirectly through its water retentive and insulative capacities.

The preservation or replacement of the surface organic layer is often considered the most important factor in native plant revegetation (Janz 1973; Kershaw 1983; Shaver *et al.* 1983). Others recommend replacing organic soil on disturbed surfaces (McGraw 1980; Gartner *et al.* 1983; Johnson 1987). Differences between revegetation in borrow pits and on vehicle tracks in the present study also confirm that compaction, rather than removal of the organic layer, will have less detrimental effects. Especially on multiple tracks, disturbance was moderate enough to slightly compress the soil which increased plant growth indirectly through warmer, wetter soils with greater organic matter.

Short-term effects on soil conditions and plant species composition have already been considered in improving construction practises in the North. Attention should also be given to the long-term effects of revegetation and soil development on disturbed sites. Construction planners should take note that the effects of removing all vegetation and soil layers in shrub tundra may last for centuries; decades may be required for even the establishment of a

sparse shrub layer. Efforts to preserve the organic and other soil layers may eventually lead to increased plant cover and species richness.

Scientific Contributions

This is one of the first comprehensive long-term revegetation studies on disturbances more than 35 years following abandonment in the Arctic. The focus on the differences in disturbance types and the comparison between two stages in successional development are also unique. These objectives provide insight into revegetation and soil development in primary and secondary succession.

Preliminary results from the comparison between the 1978 and 1993 data from the CANOL corridor provide evidence of subtle changes in species composition during successional development. Replication of this study after another fifteen years would provide a direct comparison and more reliable results. Substantial insight into primary and secondary succession in the CANOL corridor could be gained by such a study. Similar investigations in different plant communities would test the applicability of these results to other tundra environments in the Low Arctic.

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	Undisturbed			Borrow Pits			Linear Disturbances		
	East	West	All	East	West	All	East	West	All
n	150	105	255	120	90	210	165	60	225
woody plants									
Arctostaphylos rubra	2.58	0.00	**1.52**	0.00	0.00	**0.00**	0.35	0.00	**0.25**
Betula glandulosa	24.70	30.39	**27.04**	6.61	0.73	**4.09**	18.57	16.75	**18.08**
Cassiope tetragona	0.00	0.48	**0.20**	*	0.00	*	0.01	*	**0.00**
Cornus canadensis	0.67	0.32	**0.53**	*	0.00	*	0.68	1.23	**0.83**
Empetrum nigrum	13.71	3.88	**9.66**	3.16	*	**1.80**	11.65	14.28	**12.35**
Ledum spp.	0.23	0.24	**0.24**	0.03	*	**0.01**	0.11	0.37	**0.18**
Picea glauca	0.00	0.01	**0.00**	0.00	0.00	**0.00**	*	*	*
Populus balsamifera	0.00	0.01	**0.00**	0.13	*	**0.07**	*	0.00	*
Potentilla fruticosa	0.21	0.00	**0.12**	*	0.00	*	0.76	0.00	**0.56**
Rubus acaulis	0.16	*	**0.09**	0.12	0.00	**0.07**	0.66	0.00	**0.48**
Rubus Chamaemorus	1.47	0.08	**0.89**	0.01	0.00	**0.00**	0.48	0.00	**0.35**
Salix alaxensis	0.00	0.00	**0.00**	0.00	0.11	**0.05**	*	0.00	*
Salix arbusculoides	0.20	0.00	**0.12**	0.35	0.00	**0.20**	0.02	0.00	**0.01**
Salix arb. x plan.	3.43	*	**2.02**	0.00	0.00	**0.00**	2.31	0.12	**1.72**
Salix arctica	0.00	0.00	**0.00**	0.01	0.00	**0.00**	0.00	0.00	**0.00**
Salix commutata	0.00	*	*	0.05	0.00	**0.03**	0.00	0.00	**0.00**
Salix lanata	0.17	0.00	**0.10**	0.00	0.00	**0.00**	1.70	0.00	**1.25**
Salix myrtillifolia	0.00	0.00	**0.00**	0.00	0.00	**0.00**	*	0.00	*
Salix plan./glau.	1.55	0.01	**0.91**	3.56	1.38	**2.62**	5.08	4.87	**5.03**
Salix reticulata	6.31	0.00	**3.71**	*	0.00	*	4.65	*	**3.41**
Salix sp.	0.00	0.48	**0.20**	0.02	*	**0.01**	0.01	0.08	**0.03**
total Salix	11.65	0.49	**7.05**	3.98	1.49	**2.91**	13.78	5.07	**11.46**
Sibbaldia procumbens	0.01	*	**0.01**	1.02	0.02	**0.59**	0.22	2.68	**0.88**
Spiraea beauverdiana	0.46	0.06	**0.29**	0.37	0.00	**0.21**	0.76	0.12	**0.59**
Vaccinium uliginosum	7.73	0.06	**4.57**	0.60	0.00	**0.34**	5.57	0.50	**4.22**
Vaccinium vitis-idaea	1.93	2.77	**2.28**	0.18	0.06	**0.13**	1.21	0.92	**1.13**

forbs									
Anemone narcissiflora	0.04	0.00	**0.02**	0.00	0.00	**0.00**	0.08	0.00	**0.06**
Anemone parviflora	0.04	0.00	**0.02**	0.00	*	*	0.06	0.00	**0.04**
Anemone Richardsonii	0.36	0.00	**0.21**	0.00	0.00	**0.00**	0.31	0.00	**0.23**
Antennaria spp.	0.07	0.20	**0.13**	1.88	0.10	**1.12**	0.10	0.53	**0.22**
Arnica Lessingii	0.00	0.00	**0.00**	0.02	0.00	**0.01**	0.00	0.00	**0.00**
Artemisia arctica	0.25	0.01	**0.15**	1.66	0.09	**0.99**	2.74	2.68	**2.72**
Artemisia Tilesii	*	0.00	*	0.00	0.00	**0.00**	0.01	0.00	**0.01**
Aster sibiricus	0.00	0.00	**0.00**	0.01	*	**0.00**	0.00	0.00	**0.00**
Astragalus umbellatus	0.00	0.00	**0.00**	0.00	0.00	**0.00**	0.05	0.00	**0.04**
Cerastium Beeringia.	0.00	0.00	**0.00**	0.02	0.00	**0.01**	0.01	0.00	**0.01**
Epilobium anagallid.	0.00	0.00	**0.00**	0.47	0.00	**0.27**	0.14	0.03	**0.11**
Epilobium angust.	0.04	0.07	**0.05**	0.70	0.44	**0.59**	0.62	0.42	**0.57**
Epilobium latifolium	0.00	0.00	**0.00**	0.01	0.01	**0.01**	0.00	0.00	**0.00**
Gentiana sp.	*	0.00	*	0.04	*	**0.02**	0.00	0.03	**0.01**
Linnaea borealis	0.63	0.00	**0.37**	0.00	0.00	**0.00**	0.01	0.00	**0.01**
Mertensia paniculata	0.00	*	*	0.01	*	**0.00**	0.05	0.00	**0.04**
Moneses uniflora	0.00	0.00	**0.00**	0.00	*	*	0.00	0.00	**0.00**
Parnassia Kotzebuei	0.00	0.00	**0.00**	0.07	0.00	**0.04**	0.02	0.00	**0.01**
Pedicularis cap./sud.	0.00	0.00	**0.00**	0.00	0.00	**0.00**	0.02	0.00	**0.01**
Pedicularis labrador.	0.32	0.02	**0.20**	0.01	0.00	**0.00**	0.04	0.03	**0.04**
Petasites frigidus	1.15	*	**0.67**	0.06	0.00	**0.03**	1.02	0.10	**0.78**
Polemonium acutiflor.	0.23	0.00	**0.13**	0.03	0.00	**0.01**	0.36	0.03	**0.28**
Polygonum viviparum	*	*	*	0.03	0.00	**0.01**	0.02	0.00	**0.01**
Pyrola spp.	0.04	0.00	**0.02**	0.53	*	**0.30**	0.30	0.47	**0.35**
Rumex arcticus	*	0.00	*	0.02	0.00	**0.01**	0.03	0.00	**0.02**
Rhodiolia integrifol.	*	*	*	0.32	0.00	**0.18**	0.17	0.00	**0.12**
Sagina Linnaei	0.00	0.00	**0.00**	1.11	0.00	**0.63**	0.04	0.00	**0.03**
Saxifraga tricuspid.	0.00	0.00	**0.00**	0.00	0.02	**0.01**	0.00	0.00	**0.00**
Senecio triangularis	0.00	0.00	**0.00**	0.29	0.00	**0.17**	0.64	*	**0.47**
Senecio yukonensis	0.00	*	*	0.03	0.00	**0.02**	0.02	0.10	**0.04**
Senecio spp.	0.15	0.00	**0.09**	0.44	*	**0.25**	0.09	0.00	**0.07**
Solidago multiradiata	0.02	0.00	**0.01**	*	*	*	0.42	0.00	**0.31**
Stellaria mon./long.	0.12	0.01	**0.07**	0.06	0.00	**0.03**	0.18	0.10	**0.16**
Taraxacum sp.	0.00	0.00	**0.00**	0.00	0.00	**0.00**	0.05	0.00	**0.04**
Valeriana capitata	0.02	0.00	**0.01**	0.00	0.00	**0.00**	0.03	0.00	**0.02**
Veronica Wormskjoldii	0.01	0.00	**0.00**	0.58	0.00	**0.33**	0.29	0.07	**0.23**
Viola epipsila	0.00	0.00	**0.00**	0.01	0.00	**0.00**	0.00	0.00	**0.00**

forb sp.1	0.63	0.00	**0.37**	0.00	0.00	**0.00**	0.37	0.00	**0.27**
forb sp.2	0.00	0.00	**0.00**	0.00	*	*	0.00	0.00	**0.00**
forb sp.3	0.02	0.00	**0.01**	0.00	0.00	**0.00**	0.02	0.00	**0.01**
graminoids									
Agrostis scabra	0.00	0.00	**0.00**	1.68	0.01	**0.96**	0.21	0.10	**0.18**
Calamagrostis spp.	0.13	0.03	**0.09**	0.04	*	**0.02**	0.09	0.00	**0.07**
Carex aquatilis	0.25	0.00	**0.15**	0.03	0.00	**0.01**	0.61	0.02	**0.45**
Carex aurea	0.00	0.00	**0.00**	0.35	0.00	**0.20**	0.00	0.00	**0.00**
Carex spp.	0.34	0.02	**0.21**	0.54	*	**0.31**	0.47	0.08	**0.37**
total Carex	0.59	0.02	**0.35**	0.92	*	**0.52**	1.08	0.10	**0.82**
Eriophorum sp.	0.00	0.00	**0.00**	*	0.00	*	*	0.00	*
grass spp.	1.29	0.85	**1.11**	0.46	0.27	**0.38**	2.39	0.98	**2.02**
Juncus spp.	0.00	0.00	**0.00**	0.13	0.00	**0.08**	0.03	0.10	**0.05**
Luzula parviflora	0.02	0.00	**0.01**	0.23	*	**0.13**	0.30	0.05	**0.23**
Phleum alpinum	0.00	0.00	**0.00**	*	0.00	*	0.00	0.00	**0.00**
Poa spp.	0.00	0.00	**0.00**	0.27	0.00	**0.15**	0.00	0.00	**0.00**
Trisetum spicatum	0.00	0.00	**0.00**	0.44	0.07	**0.28**	0.05	0.05	**0.05**
lichens									
Alectoria ochroleuca	0.00	0.00	**0.00**	0.00	0.04	**0.02**	0.03	0.00	**0.02**
Cetraria com./hep.	0.00	0.00	**0.00**	0.00	0.01	**0.00**	0.00	0.00	**0.00**
Cetraria cucullata	*	0.26	**0.11**	0.00	0.06	**0.02**	0.00	0.07	**0.02**
Cetraria ericetorum	0.00	0.02	**0.01**	0.00	0.00	**0.00**	0.00	0.00	**0.00**
Cetraria islandica	0.13	0.64	**0.34**	0.05	0.09	**0.07**	0.08	1.98	**0.59**
Cetraria nigricans	0.00	0.02	**0.01**	0.00	0.13	**0.06**	0.00	0.00	**0.00**
Cetraria nivalis	*	1.67	**0.69**	0.00	0.59	**0.25**	0.00	0.27	**0.07**
Cetraria pinastri	1.02	1.24	**1.11**	0.04	0.72	**0.33**	0.52	0.42	**0.49**
Cetraria richardsonii	0.00	0.12	**0.05**	0.00	0.00	**0.00**	0.00	0.37	**0.10**
Cetraria sp.	0.06	0.00	**0.04**	0.00	0.00	**0.00**	0.00	0.00	**0.00**
total Cetraria	1.21	3.96	**2.35**	0.09	1.60	**0.74**	0.60	3.10	**1.27**
Cladina arbuscula	0.78	3.06	**1.72**	0.07	0.58	**0.29**	0.24	0.58	**0.33**
Cladina mitis	0.01	0.01	**0.01**	0.01	0.03	**0.02**	0.00	0.02	**0.00**
Cladina rangiferina	3.77	7.34	**5.24**	0.00	0.10	**0.04**	0.81	0.57	**0.74**
Cladina stellaris	3.81	31.92	**15.39**	0.01	0.11	**0.05**	0.70	7.62	**2.54**
total Cladina	8.37	42.33	**22.53**	0.08	0.82	**0.40**	1.74	8.78	**3.62**
Cladonia amaurocraea	0.00	0.68	**0.82**	0.00	0.10	**0.04**	0.01	0.02	**0.01**
Cladonia cariosa	0.00	0.06	**0.02**	0.11	0.20	**0.15**	0.02	0.03	**0.03**
Cladonia cenotea	0.03	0.16	**0.08**	0.08	0.12	**0.10**	0.05	0.25	**0.10**
Cladonia cervicornal.	0.00	0.00	**0.00**	0.75	0.18	**0.50**	0.04	0.42	**0.14**

Cladonia cocc./bell.	0.05	0.75	**0.34**	0.17	0.09	**0.13**	0.07	0.12	**0.08**
Cladonia crispata	0.00	0.29	**0.12**	0.00	0.00	**0.00**	0.01	0.13	**0.04**
Cladonia macrophylla	0.00	0.27	**0.11**	0.23	0.34	**0.28**	0.17	0.10	**0.15**
Cladonia pocillum	0.00	0.00	**0.00**	0.02	0.00	**0.01**	0.00	0.00	**0.00**
Cladonia sulphurina	0.03	0.40	**0.18**	0.02	0.17	**0.08**	0.01	0.18	**0.06**
Cladonia uncialis	0.25	1.00	**0.56**	0.12	0.27	**0.18**	0.15	0.12	**0.14**
Cladonia tapered	0.89	3.47	**1.95**	1.08	1.31	**1.18**	0.67	1.67	**0.94**
Cladonia cup	0.09	0.26	**0.16**	0.77	1.01	**0.87**	0.25	0.95	**0.44**
Cladonia sp.3	0.00	0.00	**0.00**	0.07	0.00	**0.04**	0.00	0.00	**0.00**
Cladonia sp.4	0.01	0.16	**0.07**	0.00	0.00	**0.00**	0.08	0.00	**0.06**
total Cladonia	1.33	7.49	**3.87**	3.41	3.79	**3.57**	1.53	3.98	**2.19**
Dactylina arctica	0.01	0.00	**0.00**	0.00	0.00	**0.00**	0.03	*	**0.02**
Nephroma arcticum	1.79	0.02	**1.06**	0.00	0.00	**0.00**	0.58	*	**0.42**
Pannaria pezizoides	0.00	0.00	**0.00**	0.27	0.03	**0.17**	0.04	0.00	**0.03**
Parmelia sp.	0.11	0.00	**0.06**	0.00	0.01	**0.00**	0.00	0.00	**0.00**
Parmeliop. hyperopta	1.49	1.96	**1.69**	0.02	0.00	**0.01**	0.70	0.62	**0.68**
Peltigera aphthosa	1.76	0.01	**1.04**	1.54	0.49	**1.09**	3.57	0.82	**2.84**
Peltigera canina	0.00	0.00	**0.00**	0.26	0.68	**0.44**	0.08	0.00	**0.06**
Peltigera malacea	0.00	0.01	**0.00**	0.01	0.08	**0.04**	0.22	0.15	**0.20**
Peltigera polydactyla	1.15	0.11	**0.73**	0.07	0.07	**0.07**	0.52	0.05	**0.39**
Peltigera rufescens	0.03	0.00	**0.02**	0.02	0.00	**0.01**	0.31	0.00	**0.23**
Peltigera venosa	0.00	0.00	**0.00**	0.01	0.00	**0.00**	0.00	0.00	**0.00**
Peltigera sp.	0.07	0.00	**0.04**	0.05	0.00	**0.03**	0.08	0.05	**0.07**
total Peltigera	3.01	0.13	**1.83**	1.95	1.31	**1.68**	4.78	1.07	**3.79**
Psoroma hypnorum	0.00	0.00	**0.00**	0.25	0.88	**0.52**	0.08	0.00	**0.06**
Solorina crocea	0.00	0.15	**0.06**	0.57	0.26	**0.43**	0.15	2.62	**0.80**
Stereocaulon spp	0.02	5.48	**2.27**	25.24	6.12	**17.05**	3.36	10.62	**5.30**
Thamnolina sp.	0.00	0.00	**0.00**	0.00	0.00	**0.00**	0.00	0.02	**0.00**
Umbilicaria spp.	0.00	*	*	0.03	0.11	**0.06**	0.01	0.18	**0.06**
crustose	0.00	2.73	**1.13**	5.74	2.99	**4.56**	1.36	1.75	**1.47**
bryophytes									
Aulacomnium palustre	8.67	0.06	**5.13**	1.61	0.01	**0.92**	10.01	0.37	**7.44**
Buxbaumia aphylla	0.00	0.01	**0.00**	0.01	0.00	**0.00**	0.00	0.00	**0.00**
Climacium dendroides	0.02	0.00	**0.01**	0.00	0.00	**0.00**	0.05	0.00	**0.04**
Dicranum spp.	1.69	6.07	**3.49**	0.49	0.03	**0.30**	1.05	3.25	**1.64**
Drepanocladus sp.1	0.00	0.00	**0.00**	2.69	0.00	**1.54**	0.98	0.00	**0.72**
Drepanocladus sp.2	0.06	0.00	**0.04**	0.65	0.03	**0.39**	1.89	2.95	**2.17**
Hylocomnium splendens	17.14	0.00	**10.08**	0.02	0.00	**0.01**	7.75	0.03	**5.69**

Leptobryum pyriforme	0.00	0.00	**0.00**	0.00	0.00	**0.00**	0.01	0.00	**0.00**
Pleurozium schreberi	14.83	18.30	**16.26**	0.11	0.01	**0.07**	6.30	7.15	**6.52**
Polytrichum com./jun.	9.51	13.38	**11.11**	1.53	3.88	**2.54**	5.59	14.78	**8.04**
Polytrichum piliferum	0.00	0.07	**0.03**	0.88	11.67	**5.50**	0.12	4.58	**1.31**
Polytrichum strictum	7.29	5.20	**6.43**	0.44	0.00	**0.25**	2.33	1.22	**2.04**
total Polytrichum	16.80	18.65	**17.56**	2.86	15.54	**8.30**	8.04	20.58	**11.39**
Rhacomitrum canescens	0.11	0.00	**0.06**	2.68	0.09	**1.57**	0.01	1.20	**0.32**
Rhizomnium spp.	0.57	0.00	**0.34**	0.00	0.00	**0.00**	1.79	0.00	**1.31**
Sphagnum spp.	10.83	0.00	**6.37**	0.00	0.00	**0.00**	2.70	0.00	**1.98**
Tomenthypnum nitens	4.31	0.00	**2.54**	0.00	0.00	**0.00**	3.91	0.00	**2.87**
pleurocarpic spp.	0.07	0.00	**0.04**	0.09	0.07	**0.08**	2.13	0.00	**1.56**
acrocarpic moss	0.19	0.21	**0.20**	3.15	1.96	**2.64**	1.21	0.95	**1.14**
total pleurocarpic	46.90	24.43	**37.65**	8.33	0.24	**4.87**	34.08	14.95	**28.98**
liverwort	3.19	1.92	**2.67**	3.44	0.01	**1.97**	9.52	15.00	**10.98**
other plant species									
Botrychium Lunaria	0.00	0.00	**0.00**	0.00	*	*	0.00	0.00	**0.00**
Equisetum arvense	0.26	0.00	**0.15**	0.14	0.00	**0.08**	0.42	0.00	**0.31**
Equisetum scirpoides	0.35	0.00	**0.21**	0.00	0.00	**0.00**	0.21	0.00	**0.16**
Equisetum sylvaticum	1.79	0.00	**1.05**	0.20	0.00	**0.11**	0.95	0.00	**0.69**
total Equisetum	2.40	0.00	**1.41**	0.34	0.00	**0.20**	1.58	0.00	**1.16**
Lycopodium alp./comp.	0.00	*	*	*	0.16	**0.07**	0.00	*	*
Lycopodium ann./clav.	0.00	0.01	**0.00**	0.23	*	**0.13**	1.07	0.47	**0.91**
Lycopodium Selago	0.00	0.00	**0.00**	0.03	0.00	**0.01**	0.00	0.00	**0.00**
total Lycopodium	0.00	0.01	**0.00**	0.26	0.16	**0.21**	1.07	0.47	**0.91**
algae	0.01	0.00	**0.00**	1.55	0.00	**0.89**	0.05	0.00	**0.04**

Appendix 2. Average frequency (%) for all species found in undisturbed areas, borrow pits and linear disturbances. Data are subdivided within each disturbance category between sites east and west of the main camp. Species observed within a site but outside the quadrats are indicated with an asterisk (*). Some species are grouped together into genera or other taxonomic groups.

	Undisturbed			Borrow Pits			Linear Disturbances		
	East	West	All	East	West	All	East	West	All
woody plants									
Arctostaphylos rubra	12	0	7	0	0	0	3	0	2
Betula glandulosa	89	89	89	54	8	34	84	77	82
Cassiope tetragona	0	2	1	*	0	*	1	*	0
Cornus canadensis	21	9	16	*	0	*	13	23	16
Empetrum nigrum	65	15	45	21	0	12	56	43	53
Ledum spp.	7	3	5	2	0	1	4	8	5
Picea glauca	0	1	0	0	0	0	*	*	*
Populus balsamifera	0	0	0	1	*	0	*	0	*
Potentilla fruticosa	4	0	2	*	0	*	8	0	6
Rubus acaulis	10	*	6	4	0	2	28	0	21
Rubus Chamaemorus	36	4	23	1	0	0	12	0	8
Salix alaxensis	0	0	0	0	3	1	*	0	*
Salix arbusculoides	1	0	0	6	0	3	1	0	0
Salix arb. x plan.	15	*	9	1	0	0	12	3	10
Salix arctica	0	0	0	1	0	0	0	0	0
Salix commutata	0	*	*	3	0	1	0	0	0
Salix lanata	2	0	1	0	0	0	6	0	4
Salix myrtillifolia	0	0	0	0	0	0	*	0	*
Salix plan./glau.	5	1	4	53	14	37	39	30	37
Salix reticulata	23	0	13	*	0	*	22	*	16
Salix sp.	0	1	0	2	*	1	1	2	1
Sibbaldia procumbens	1	*	1	28	2	17	12	33	18
Spiraea beauverdiana	10	3	7	19	0	11	18	7	15
Vaccinium uliginosum	45	3	27	10	0	6	36	17	31
Vaccinium vitis-idaea	79	89	83	8	2	6	51	40	48
forbs									
Anemone narcissiflora	2	0	1	0	0	0	2	0	2
Anemone parviflora	2	0	1	0	*	*	5	0	4
Anemone Richardsonii	11	0	7	0	0	0	13	0	10

Antennaria spp.	3	2	2	48	2	28	8	10	8
Arnica Lessingii	0	0	0	2	0	1	0	0	0
Artemisia arctica	9	1	5	21	3	13	26	32	28
Artemisia Tilesii	*	0	*	0	0	0	1	0	1
Aster sibiricus	0	0	0	1	*	0	0	0	0
Astragalus umbellatus	0	0	0	0	0	0	1	0	0
Cerastium Beeringia.	0	0	0	2	0	1	1	0	1
Epilobium anagallid.	0	0	0	38	0	21	12	3	9
Epilobium angust.	1	2	1	28	8	19	24	18	22
Epilobium latifolium	0	0	0	1	1	1	0	0	0
Gentiana sp.	*	0	*	2	*	1	0	3	1
Linnaea borealis	21	0	13	0	0	0	1	0	1
Mertensia paniculata	0	*	*	1	*	0	2	0	1
Moneses uniflora	0	0	0	0	*	*	0	0	0
Parnassia Kotzebuei	0	0	0	5	0	3	2	0	1
Pedicularis cap./sud.	0	0	0	0	0	0	1	0	0
Pedicularis labrador.	9	1	5	1	0	0	3	2	3
Petasites frigidus	21	*	12	2	0	1	24	8	20
Polemonium acutiflor.	13	0	7	2	0	1	15	3	12
Polygonum viviparum	*	*	*	2	0	1	1	0	1
Pyrola spp.	3	0	2	18	*	10	16	12	15
Rumex arcticus	*	0	*	1	0	0	2	0	1
Rhodiolia integrifol.	*	*	*	13	0	8	5	0	4
Sagina Linnaei	0	0	0	40	0	23	3	0	2
Saxifraga tricuspid.	0	0	0	0	1	0	0	0	0
Senecio triangularis	0	0	0	2	0	1	12	*	8
Senecio yukonensis	0	*	*	3	0	1	1	5	2
Senecio spp.	3	0	2	21	*	12	5	0	4
Solidago multiradiata	1	0	0	*	*	*	9	0	7
Stellaria mon./long.	11	1	7	5	0	3	19	7	16
Taraxacum sp.	0	0	0	0	0	0	2	0	1
Valeriana capitata	1	0	1	0	0	0	2	0	1
Veronica Wormskjoldii	1	0	0	37	0	21	21	3	16
Viola epipsila	0	0	0	1	0	0	0	0	0
forb sp.1	18	0	11	0	0	0	16	0	12
forb sp.2	0	0	0	0	*	*	0	0	0
forb sp.3	2	0	1	0	0	0	2	0	1

graminoids									
Agrostis scabra	0	0	0	55	1	32	13	12	12
Calamagrostis spp.	11	3	8	1	*	0	7	0	5
Carex aquatilis	5	0	3	3	0	1	20	2	15
Carex aurea	0	0	0	7	0	4	0	0	0
Carex spp.	15	1	9	8	*	5	16	7	14
Eriophorum sp.	0	0	0	*	0	*	*	0	*
grass spp.	74	47	63	18	16	17	72	57	68
Juncus spp.	0	0	0	12	0	7	3	5	4
Luzula parviflora	2	0	1	8	*	5	18	5	15
Phleum alpinum	0	0	0	*	0	*	0	0	0
Poa spp.	0	0	0	11	0	6	0	0	0
Trisetum spicatum	0	0	0	31	1	18	5	5	5
lichens									
Alectoria ochroleuca	0	0	0	0	4	2	1	0	0
Cetraria com./hep.	0	0	0	0	1	0	0	0	0
Cetraria cucullata	*	18	7	0	6	2	0	5	1
Cetraria ericetorum	0	2	1	0	0	0	0	0	0
Cetraria islandica	5	23	12	3	3	3	4	43	15
Cetraria nigricans	0	2	1	0	3	1	0	0	0
Cetraria nivalis	*	31	13	0	23	10	0	15	4
Cetraria pinastri	85	73	80	4	50	24	45	40	44
Cetraria richardsonii	0	5	2	0	0	0	0	5	1
Cetraria sp.	5	0	3	0	0	0	0	0	0
Cladina arbuscula	11	36	22	2	20	10	9	23	13
Cladina mitis	1	1	1	1	3	2	0	2	0
Cladina rangiferina	38	48	42	0	10	4	15	23	17
Cladina stellaris	21	83	47	1	7	3	14	45	22
Cladonia amaurocraea	0	15	6	0	6	2	1	2	1
Cladonia cariosa	0	3	1	10	13	11	2	3	3
Cladonia cenotea	3	10	6	6	7	6	2	15	5
Cladonia cervicornal.	0	0	0	39	11	27	2	13	5
Cladonia cocc./bell.	1	20	9	9	8	9	3	12	5
Cladonia crispata	0	10	4	0	0	0	1	3	1
Cladonia macrophylla	0	10	4	10	14	12	7	7	7
Cladonia pocillum	0	0	0	2	0	1	0	0	0
Cladonia sulphurina	3	22	11	2	7	4	1	17	5
Cladonia uncialis	4	23	12	4	17	10	5	5	5

Cladonia tapered	39	83	57	52	47	50	37	75	47
Cladonia cup	8	14	11	62	54	59	19	55	29
Cladonia sp.3	0	0	0	2	0	1	0	0	0
Cladonia sp.4	1	7	3	0	0	0	4	0	3
Dactylina arctica	1	0	0	0	0	0	1	*	1
Nephroma arcticum	7	2	5	0	0	0	5	*	4
Pannaria pezizoides	0	0	0	24	1	14	4	0	3
Parmelia sp.	2	0	1	0	1	0	0	0	0
Parmeliop. hyperopta	83	72	78	2	0	1	34	27	32
Peltigera aphthosa	15	1	9	14	11	13	23	20	22
Peltigera canina	0	0	0	5	12	8	2	0	2
Peltigera malacea	0	1	0	1	2	1	4	5	4
Peltigera polydactyla	9	2	6	3	2	3	7	3	6
Peltigera rufescens	1	0	1	1	0	0	4	0	3
Peltigera venosa	0	0	0	1	0	0	0	0	0
Peltigera sp.	2	0	1	2	0	1	3	5	4
Psoroma hypnorum	0	0	0	19	18	19	5	0	4
Solorina crocea	0	2	1	16	12	14	3	40	13
Stereocaulon spp.	1	25	11	76	79	77	25	62	35
Thamnolina sp.	0	0	0	0	0	0	0	2	0
Umbilicaria spp.	0	*	*	2	10	5	1	3	1
crustose	0	14	6	71	71	71	12	27	16
bryophytes									
Aulacomnium palustre	50	2	30	11	1	7	62	5	47
Buxbaumia aphylla	0	1	0	1	0	0	0	0	0
Climacium dendroides	1	0	0	0	0	0	1	0	1
Dicranum spp.	31	51	40	19	2	12	28	28	28
Drepanocladus sp.1	0	0	0	8	0	4	5	0	4
Drepanocladus sp.2	3	0	2	9	1	6	25	10	21
Hylocomnium splendens	52	0	31	1	0	0	43	2	32
Leptobryum pyriforme	0	0	0	0	0	0	1	0	0
Pleurozium schreberi	54	43	49	8	1	5	31	35	32
Polytrichum com./jun.	43	70	54	43	53	48	44	77	53
Polytrichum piliferum	0	3	1	26	58	40	7	33	14
Polytrichum strictum	34	40	36	3	0	1	19	18	19
Rhacomitrum canescens	1	0	1	18	8	13	1	12	4
Rhizomnium spp.	9	0	5	0	0	0	16	0	12
Sphagnum spp.	35	0	21	0	0	0	18	0	13

Tomenthypnum nitens	18	0	**11**	0	0	**0**	21	0	**16**
pleurocarpic spp.	4	0	**2**	3	3	**3**	25	0	**18**
acrocarpic moss	5	10	**7**	66	67	**66**	26	40	**30**
liverwort	41	46	**43**	48	1	**28**	66	73	**68**
other plant species									
Botrychium Lunaria	0	0	**0**	0	*	*	0	0	**0**
Equisetum arvense	10	0	**6**	12	0	**7**	30	0	**22**
Equisetum scirpoides	33	0	**20**	0	0	**0**	21	0	**16**
Equisetum sylvaticum	50	0	**29**	11	0	**6**	41	0	**30**
Lycopodium alp./comp.	0	*	*	*	3	**1**	0	*	*
Lycopodium ann./clav.	0	1	**0**	2	*	**1**	10	7	**9**
Lycopodium Selago	0	0	**0**	1	0	**0**	0	0	**0**
algae	1	0	**0**	21	0	**12**	2	0	**2**

Appendix 3. Average cover (%) for species in different types of linear disturbances. Species observed within a site but outside the quadrats are indicated with an asterisk (*). Some species are grouped together into genera or other taxonomic groups. n = # of quadrats.

	Linear Disturbances						
	East				West		
	Access	Track	Bladed	Multi	Track	Heavy	All
n	45	45	45	30	30	30	225
woody plants							
Arctostaphylos rubra	0.07	0.78	0.00	0.63	0.00	0.00	**0.25**
Betula glandulosa	25.38	15.36	17.49	14.80	10.57	22.93	**18.08**
Cassiope tetragona	0.02	0.00	0.00	*	*	*	**0.00**
Cornus canadensis	0.22	0.44	1.82	0.00	0.53	1.93	**0.83**
Empetrum nigrum	13.60	22.31	5.47	2.00	8.53	20.03	**12.35**
Ledum spp.	0.02	0.22	0.04	0.17	0.00	0.73	**0.18**
Picea glauca	*	0.00	0.00	0.00	0.00	*	*
Populus balsamifera	*	0.00	0.00	0.00	0.00	0.00	*
Potentilla fruticosa	0.00	2.67	*	0.20	0.00	0.00	**0.56**
Rubus acaulis	0.24	0.51	0.98	1.03	0.00	0.00	**0.48**
Rubus Chamaemorus	*	1.67	0.09	0.00	0.00	0.00	**0.35**
Salix alaxensis	0.00	0.00	*	0.00	0.00	0.00	*
Salix arbusculoides	0.07	0.00	0.00	0.00	0.00	0.00	**0.01**
Salix arb. x plan.	1.67	2.44	0.67	5.53	0.23	0.00	**1.72**
Salix lanata	0.00	0.78	0.00	8.20	0.00	0.00	**1.25**
Salix myrtillifolia	0.00	*	0.00	0.00	0.00	0.00	*
Salix plan./glau.	4.89	0.09	9.58	6.13	0.13	9.60	**5.03**
Salix reticulata	0.04	5.91	0.00	16.67	0.00	0.00	**3.41**
Salix sp.	0.04	0.00	0.00	0.00	0.00	0.17	**0.03**
total Salix	6.71	9.22	10.24	36.53	0.37	9.77	**11.46**
Sibbaldia procumbens	0.29	0.02	0.49	0.03	0.23	5.13	**0.88**
Spiraea beauverdiana	2.76	*	0.02	0.00	0.00	0.23	**0.59**
Vaccinium uliginosum	2.27	7.71	0.93	14.27	0.67	0.13	**4.22**
Vaccinium vitis-idaea	0.80	1.93	1.40	0.43	0.83	1.00	**1.13**
forbs							
Anemone narcissiflora	0.00	0.31	0.00	0.00	0.00	0.00	**0.06**
Anemone parviflora	0.00	0.13	0.00	0.13	0.00	0.00	**0.04**
Anemone Richardsonii	0.00	0.02	0.00	1.67	0.00	0.00	**0.23**

Antennaria spp.	0.11	0.11	0.16	0.00	0.07	1.00	0.22
Artemisia arctica	5.84	0.16	2.64	2.10	1.07	4.30	2.72
Artemisia Tilesii	0.00	0.00	0.00	0.07	0.00	0.00	0.01
Astragalus umbellatus	0.00	0.00	0.00	0.27	0.00	0.00	0.04
Cerastium Beeringia.	0.00	0.00	0.04	0.00	0.00	0.00	0.01
Epilobium anagallid.	0.16	0.09	0.27	0.00	0.00	0.07	0.11
Epilobium angust.	1.38	0.13	0.78	*	0.00	0.83	0.57
Gentiana sp.	0.00	0.00	0.00	0.00	0.00	0.07	0.01
Linnaea borealis	0.02	0.00	0.00	0.03	0.00	0.00	0.01
Mertensia paniculata	0.07	0.11	0.00	*	0.00	0.00	0.04
Parnassia Kotzebuei	0.00	*	0.07	0.00	0.00	0.00	0.01
Pedicularis cap./sud.	0.00	0.00	0.00	0.10	0.00	0.00	0.01
Pedicularis labrador.	*	0.13	0.00	0.03	0.07	*	0.04
Petasites frigidus	0.44	0.51	0.76	3.07	0.00	0.20	0.78
Polemonium acutiflor.	*	0.02	0.91	0.60	0.00	0.07	0.28
Polygonum viviparum	0.02	0.04	0.00	*	0.00	0.00	0.01
Pyrola spp.	0.76	0.07	0.20	0.13	0.13	0.80	0.35
Rumex arcticus	0.00	*	0.11	*	0.00	0.00	0.02
Rhodiolia integrifol.	0.51	0.07	0.04	0.00	0.00	0.00	0.12
Sagina Linnaei	0.04	0.00	0.11	0.00	0.00	0.00	0.03
Senecio triangularis	1.96	*	0.38	*	0.00	*	0.47
Senecio yukonensis	0.07	0.00	0.00	0.00	*	0.20	0.04
Senecio spp.	0.00	0.13	0.20	*	0.00	0.00	0.07
Solidago multiradiata	0.62	*	0.62	0.43	0.00	0.00	0.31
Stellaria mon./long.	0.07	0.02	0.44	0.20	0.00	0.20	0.16
Taraxacum sp.	0.20	0.00	0.00	0.00	0.00	0.00	0.04
Valeriana capitata	0.00	0.02	0.00	0.13	0.00	0.00	0.02
Veronica Wormskjoldii	0.49	0.04	0.42	0.17	0.00	0.13	0.23
forb sp.1	0.00	0.62	0.00	1.10	0.00	0.00	0.27
forb sp.3	0.00	*	0.00	0.10	0.00	0.00	0.01
graminoids							
Agrostis scabra	0.22	0.23	0.16	0.00	0.00	0.20	0.18
Calamagrostis spp.	*	*	0.18	0.23	0.00	0.00	0.07
Carex aquatilis	*	1.24	0.29	1.07	0.00	0.03	0.45
Carex spp.	0.16	0.38	0.20	1.50	0.03	0.13	0.37
total Carex	0.16	1.62	0.49	2.57	0.03	0.17	0.82
Eriophorum sp.	0.00	0.00	*	0.00	0.00	0.00	*
grass spp.	3.53	0.89	2.13	3.33	1.33	0.63	2.02

Juncus spp.	*	*	0.11	0.00	0.00	0.20	0.05
Luzula parviflora	0.47	0.09	0.47	0.10	0.03	0.07	0.23
Trisetum spicatum	0.09	0.02	0.09	*	0.00	0.10	0.05
lichens							
Alectoria ochroleuca	0.00	0.11	0.00	0.00	0.00	0.00	0.02
Cetraria cucullata	0.00	0.00	0.00	0.00	0.13	0.00	0.02
Cetraria islandica	0.02	0.22	0.04	0.00	3.23	0.73	0.59
Cetraria nivalis	0.00	0.00	0.00	0.00	0.53	0.00	0.07
Cetraria pinastri	0.29	0.64	0.56	0.63	0.47	0.37	0.49
Cetraria richardsonii	0.00	0.00	0.00	0.00	0.67	0.07	0.10
total Cetraria	0.31	0.87	0.60	0.63	5.03	1.17	1.27
Cladina arbuscula	0.09	0.24	0.53	0.00	0.87	0.30	0.33
Cladina mitis	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Cladina rangiferina	0.04	2.07	0.84	0.00	1.07	0.07	0.74
Cladina stellaris	0.00	2.22	0.27	0.10	14.40	0.83	2.54
total Cladina	0.13	4.53	1.64	0.10	16.33	1.23	3.62
Cladonia amaurocraea	0.00	0.00	0.02	0.00	0.03	0.00	0.01
Cladonia cariosa	0.07	0.02	0.00	0.00	0.07	0.00	0.03
Cladonia cenotea	0.00	0.02	0.16	0.00	0.20	0.30	0.10
Cladonia cervicornal.	0.07	0.00	0.07	0.00	0.27	0.57	0.14
Cladonia cocc./bell.	0.00	0.07	0.20	0.00	0.03	0.20	0.08
Cladonia crispata	0.00	0.04	0.00	0.00	0.23	0.03	0.04
Cladonia macrophylla	0.60	0.00	0.02	0.00	0.13	0.07	0.15
Cladonia sulphurina	0.02	0.00	0.02	0.00	0.27	0.10	0.06
Cladonia uncialis	0.02	0.04	0.49	0.00	0.10	0.13	0.14
Cladonia tapered	0.62	0.53	1.20	0.17	2.37	0.97	0.94
Cladonia cup	0.42	0.11	0.36	0.03	0.70	1.20	0.44
Cladonia sp.4	0.29	0.00	0.00	0.00	0.00	0.00	0.06
total Cladonia	2.11	0.84	2.53	0.20	4.40	3.57	2.19
Dactylina arctica	0.00	0.04	0.07	0.00	0.00	*	0.02
Nephroma arcticum	0.00	1.84	0.27	0.00	0.00	*	0.42
Pannaria pezizoides	0.04	0.02	0.07	0.00	0.00	0.00	0.03
Parmeliop. hyperopta	0.22	1.00	0.93	0.63	0.67	0.57	0.68
Peltigera aphthosa	1.96	2.67	6.82	2.47	0.93	0.70	2.84
Peltigera canina	0.00	0.00	0.24	0.10	0.00	0.00	0.06
Peltigera malacea	0.00	0.00	0.80	0.00	0.00	0.30	0.20
Peltigera polydactyla	0.00	0.89	0.36	0.97	0.10	0.00	0.39
Peltigera rufescens	0.04	0.02	1.07	0.00	0.00	0.00	0.23

Peltigera sp.	0.00	0.29	0.00	0.00	0.00	0.10	0.07
total Peltigera	2.00	3.87	9.29	3.53	1.03	1.10	3.79
Psoroma hypnorum	0.20	0.02	0.04	0.03	0.00	0.00	0.06
Solorina crocea	0.53	0.00	*	0.00	2.83	2.40	0.80
Stereocaulon spp.	9.64	0.22	2.47	0.00	5.23	16.00	5.30
Thamnolina sp.	0.00	0.00	0.00	0.00	0.03	0.00	0.00
Umbilicaria spp.	0.00	0.00	0.04	0.00	0.37	*	0.06
crustose	1.47	0.33	3.20	0.00	2.53	0.97	1.47
bryophytes							
Aulacomnium palustre	2.22	15.82	9.29	14.07	0.00	0.73	7.44
Climacium dendroides	0.00	0.00	0.00	0.27	0.00	0.00	0.04
Dicranum spp.	0.36	1.58	1.47	0.67	5.63	0.87	1.64
Drepanocladus sp.1	0.00	3.60	0.00	0.00	0.00	0.00	0.72
Drepanocladus sp.2	3.04	0.09	2.91	1.33	0.03	5.87	2.17
Hylocomnium splendens	0.16	13.38	0.80	21.13	0.07	0.00	5.69
Leptobryum pyriforme	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Pleurozium schreberi	7.22	12.02	3.20	0.97	3.80	10.50	6.52
Polytrichum com./jun.	11.71	4.18	4.53	0.10	10.07	19.50	8.04
Polytrichum piliferum	0.22	0.00	0.22	0.00	6.83	2.33	1.31
Polytrichum strictum	0.11	3.80	4.60	0.07	2.13	0.30	2.04
total Polytrichum	12.04	7.98	9.36	0.17	19.03	22.13	11.39
Rhacomitrum canescens	0.00	0.00	0.02	0.00	2.37	0.03	0.32
Rhizomnium spp.	0.00	1.27	0.27	7.53	0.00	0.00	1.31
Sphagnum spp.	0.00	3.69	0.02	9.30	0.00	0.00	1.98
Tomenthypnum nitens	0.00	5.73	1.47	10.70	0.00	0.00	2.87
pleurocarpic spp.	0.27	2.78	2.18	3.87	0.00	0.00	1.56
acrocarpic moss	1.02	0.71	1.98	1.07	0.97	0.93	1.14
total pleurocarpic	13.29	55.00	21.33	53.00	11.90	18.00	28.98
liverwort	9.18	6.20	13.49	9.03	9.23	20.77	10.98
other plant species							
Equisetum arvense	0.00	0.56	0.44	0.23	0.00	0.00	0.31
Equisetum scirpoides	0.02	0.19	0.02	0.63	0.00	0.00	0.16
Equisetum sylvaticum	0.64	0.93	0.62	1.90	0.00	0.00	0.69
total Equisetum	0.67	2.18	1.09	2.77	0.00	0.00	1.16
Lycopodium alp./comp.	0.00	0.00	0.00	0.00	*	*	*
Lycopodium ann./clav.	2.58	0.02	1.33	*	0.00	0.93	0.91
total Lycopodium	2.58	0.02	1.33	0.00	0.00	0.93	0.91
algae	0.04	0.02	0.11	0.00	0.00	0.00	0.04

Appendix 4. Average frequency (%) for species in different types of linear disturbances. Species observed within a site but outside the quadrats are indicated with an asterisk (*). Some species are grouped together into genera or other taxonomic groups.

	Linear Disturbances						
	East				West		
	Access	Track	Bladed	Multi	Track	Heavy	All
woody plants							
Arctostaphylos rubra	2	4	0	7	0	0	2
Betula glandulosa	89	73	84	93	67	87	82
Cassiope tetragona	2	0	0	*	*	*	0
Cornus canadensis	2	24	20	0	10	37	16
Empetrum nigrum	71	87	33	23	30	57	53
Ledum spp.	2	7	2	7	0	17	5
Picea glauca	*	0	0	0	0	*	*
Populus balsamifera	*	0	0	0	0	0	*
Potentilla fruticosa	0	20	*	13	0	0	6
Rubus acaulis	11	27	40	40	0	0	21
Rubus Chamaemorus	*	36	7	0	0	0	8
Salix alaxensis	0	0	*	0	0	0	*
Salix arbusculoides	2	0	0	0	0	0	0
Salix arb. x plan.	4	20	7	20	7	0	10
Salix lanata	0	2	0	30	0	0	4
Salix myrtillifolia	0	*	0	0	0	0	*
Salix plan./glau.	53	4	64	33	10	50	37
Salix reticulata	2	27	0	77	0	0	16
Salix sp.	4	0	0	0	0	3	1
Sibbaldia procumbens	16	2	24	3	13	53	18
Spiraea beauverdiana	62	*	2	0	0	13	15
Vaccinium uliginosum	27	49	18	60	27	7	31
Vaccinium vitis-idaea	38	73	56	30	47	33	48
forbs							
Anemone narcissiflora	0	9	0	0	0	0	2
Anemone parviflora	0	11	0	13	0	0	4
Anemone Richardsonii	0	2	0	70	0	0	10
Antennaria spp.	9	4	16	0	7	13	8
Artemisia arctica	53	9	20	20	20	43	28

Artemisia Tilesii	0	0	0	7	0	0	1
Astragalus umbellatus	0	0	0	3	0	0	0
Cerastium Beeringia.	0	0	4	0	0	0	1
Epilobium anagallid.	16	2	24	0	0	7	9
Epilobium angust.	40	7	40	*	0	37	22
Gentiana sp.	0	0	0	0	0	7	1
Linnaea borealis	2	0	0	3	0	0	1
Mertensia paniculata	4	2	0	*	0	0	1
Parnassia Kotzebuei	0	*	7	0	0	0	1
Pedicularis cap./sud.	0	0	0	3	0	0	0
Pedicularis labrador.	*	9	0	3	3	*	3
Petasites frigidus	18	13	33	33	0	17	20
Polemonium acutiflor.	*	2	29	37	0	7	12
Polygonum viviparum	2	2	0	*	0	0	1
Pyrola spp.	40	4	11	7	7	17	15
Rumex arcticus	0	*	7	*	0	0	1
Rhodiolia integrifol.	13	4	2	0	0	0	4
Sagina Linnaei	4	0	7	0	0	0	2
Senecio triangularis	33	*	9	*	0	*	8
Senecio yukonensis	4	0	0	0	*	10	2
Senecio spp.	0	11	9	*	0	0	4
Solidago multiradiata	4	*	13	23	0	0	7
Stellaria mon./long.	7	2	47	20	0	13	16
Taraxacum sp.	7	0	0	0	0	0	1
Valeriana capitata	0	2	0	7	0	0	1
Veronica Wormskjoldii	31	4	29	17	0	7	16
forb sp.1	0	16	0	63	0	0	12
forb sp.3	0	*	0	10	0	0	1
graminoids							
Agrostis scabra	20	20	7	0	0	23	12
Calamagrostis spp.	*	*	9	23	0	0	5
Carex aquatilis	*	33	13	40	0	3	15
Carex spp.	7	24	4	37	3	10	14
Eriophorum sp.	0	0	*	0	0	0	*
grass spp.	80	51	80	80	63	50	68
Juncus spp.	*	*	11	0	0	10	4
Luzula parviflora	27	9	27	7	3	7	15
Trisetum spicatum	9	2	9	*	0	10	5

lichens							
Alectoria ochroleuca	2	1	0	0	0	0	0
Cetraria cucullata	0	4	0	0	10	0	1
Cetraria islandica	11	28	2	0	53	33	15
Cetraria nivalis	0	12	0	0	30	0	4
Cetraria pinastri	56	52	44	63	47	33	44
Cetraria richardsonii	0	1	0	0	3	7	1
Cladina arbuscula	7	16	18	0	30	17	13
Cladina mitis	0	0	0	0	0	3	0
Cladina rangiferina	36	37	16	0	40	7	17
Cladina stellaris	29	49	18	7	80	10	22
Cladonia amaurocraea	0	1	2	0	3	0	1
Cladonia cariosa	2	4	0	0	7	0	3
Cladonia cenotea	2	7	4	0	13	17	5
Cladonia cervicornal.	0	4	4	0	10	17	5
Cladonia cocc./bell.	4	5	7	0	7	17	5
Cladonia crispata	2	3	0	0	3	3	1
Cladonia macrophylla	0	3	2	0	7	7	7
Cladonia sulphurina	0	9	2	0	23	10	5
Cladonia uncialis	4	5	11	0	7	3	5
Cladonia tapered	31	53	51	17	87	63	47
Cladonia cup	9	29	24	3	60	50	29
Cladonia sp.4	0	0	0	0	0	0	3
Dactylina arctica	2	1	2	0	0	*	1
Nephroma arcticum	11	7	7	0	0	*	4
Pannaria pezizoides	2	1	7	0	0	0	3
Parmeliop. hyperopta	47	39	31	53	27	27	32
Peltigera aphthosa	16	21	40	13	30	10	22
Peltigera canina	0	0	4	7	0	0	2
Peltigera malacea	0	0	13	0	0	10	4
Peltigera polydactyla	13	11	7	7	7	0	6
Peltigera rufescens	2	1	9	0	0	0	3
Peltigera sp.	11	7	0	0	0	10	4
Psoroma hypnorum	2	1	4	3	0	0	4
Solorina crocea	0	17	*	0	43	37	13
Stereocaulon spp	9	27	27	0	53	70	35
Thamnolina sp.	0	1	0	0	3	0	0
Umbilicaria spp.	0	3	2	0	7	*	1

crustose	4	16	16	0	33	20	16
bryophytes							
Aulacomnium palustre	31	76	71	77	0	10	47
Climacium dendroides	0	0	0	7	0	0	1
Dicranum spp.	16	36	44	13	40	17	28
Drepanocladus sp.1	0	20	0	0	0	0	4
Drepanocladus sp.2	24	4	47	23	3	17	21
Hylocomnium splendens	9	69	33	70	3	0	32
Leptobryum pyriforme	2	0	0	0	0	0	0
Pleurozium schreberi	20	58	29	10	37	33	32
Polytrichum com./jun.	62	49	47	7	70	83	53
Polytrichum piliferum	16	0	9	0	37	30	14
Polytrichum strictum	2	33	31	7	27	10	19
Rhacomitrum canescens	0	0	2	0	20	3	4
Rhizomnium spp.	0	22	7	43	0	0	12
Sphagnum spp.	0	27	2	53	0	0	13
Tomenthypnum nitens	0	27	13	57	0	0	16
pleurocarpic spp.	16	20	20	53	0	0	18
acrocarpic moss	44	7	36	13	37	43	30
liverwort	58	71	71	63	80	67	68
other plant species							
Equisetum arvense	0	51	40	27	0	0	22
Equisetum scirpoides	2	31	2	63	0	0	16
Equisetum sylvaticum	33	44	24	73	0	0	30
Lycopodium alp./comp.	0	0	0	0	*	*	*
Lycopodium ann./clav.	29	2	4	*	0	13	9
algae	4	2	2	0	0	0	2

Appendix 5. Abbreviations of species used in ordinations, abbreviations used in tables, and full taxonomic names. Four-letter abbreviations are only given for species included in ordinations.

woody plant species		
Arru	*Arctostaphylos rubra*	*Arctostaphylos rubra* (Rehd. & Wils.) Fern.
Begl	*Betula glandulosa*	*Betula glandulosa* Michx.
	Cassiope tetragona	*Cassiope tetragona* (L.) D. Don
Coca	*Cornus canadensis*	*Cornus canadensis* L.
Emni	*Empetrum nigrum*	*Empetrum nigrum* L.
Lesp	*Ledum* spp.	*Ledum decumbens* (Ait.) Lodd. and *L. groelandicum* Oeder
	Picea glauca	*Picea glauca* (Moench) Voss
	Populus balsamifera	*Populus balsamifera* L.
Pofr	*Potentilla fruticosa*	*Potentilla fruticosa* L.
Ruac	*Rubus acaulis*	*Rubus acaulis* Michx.
Ruch	*Rubus Chamaemorus*	*Rubus Chamaemorus* L.
	Salix alaxensis	*Salix alaxensis* (Anderss.) Cov.
	Salix arbusculoides	*Salix arbusculoides* Anderss.
Saap	*Salix arb. x plan.*	*Salix arbusculoides* Anderss. *x S. planifolia* Pursh hybrid
	Salix arctica	*Salix arctica* Pall.
	Salix commutata	*Salix commutata* Bebb
	Salix lanata	*Salix lanata* L.
	Salix myrtillifolia	*Salix myrtillifolia* Anderss.
Sapg	*Salix plan./glau.*	*Salix planifolia* Pursh and *S. glauca* L., may include *Salix pulchra* Cham.
Sare	*Salix reticulata*	*Salix reticulata* L.
	Salix sp.	*Salix* sp.
Sipr	*Sibbaldia procumbens*	*Sibbaldia procumbens* L.
Spbe	*Spiraea beauverdiana*	*Spiraea beauverdiana* Schneid.
Vaul	*Vaccinium uliginosum*	*Vaccinium uliginosum* L.
Vavi	*Vaccinium vitis-idaea*	*Vaccinium vitis-idaea* L.

broad-leaved forbs		
	Anemone narcissiflora	*Anemone narcissiflora* L.
	Anemone parviflora	*Anemone parviflora* Michx.
AnRi	*Anemone Richardsonii*	*Anemone Richardsonii* Hook.
Ansp	*Antennaria* spp.	*Antennaria isolepsis* Greene, *A. monocephala* DC. and *A. stolonifera* Porsild
	Arnica Lessingii	*Arnica Lessingii* Greene
Arar	*Artemisia arctica*	*Artemisia arctica* Less.
	Artemisia Tilesii	*Artemisia Tilesii* Ledeb.
	Aster sibiricus	*Aster sibiricus* L.
	Astragalus umbellatus	*Astragalus umbellatus* Bunge
	Cerastium Beeringia.	*Cerastium Beeringianum* Cham. & Schlecht
Epan	*Epilobium anagallid.*	*Epilobium anagallidifolium* Lam.
Epat	*Epilobium angust.*	*Epilobium angustifolium* L.
Epla	*Epilobium latifolium*	*Epilobium latifolium* L.
	Gentiana sp.	*Gentiana* or *Gentianella* spp., includes *Gentiana glauca* Pall.
Libo	*Linnaea borealis*	*Linnaea borealis* L.
	Mertensia paniculata	*Mertensia paniculata* (Ait.) G. Don
	Moneses uniflora	*Moneses uniflora* (L.) Gray
	Parnassia Kotzebuei	*Parnassia Kotzebuei* Cham. & Schlect
	Pedicularis cap./sud.	*Pedicularis capitata* Adams or *P. sudetica* Willd.
Pela	*Pedicularis labrador.*	*Pedicularis labradorica* Wirsing
Pefr	*Petasites frigidus*	*Petasites frigidus* (L.) Fries
Poac	*Polemonium acutiflor.*	*Polemonium acutiflorum* Willd.
	Polygonum viviparum	*Polygonum viviparum* L.
Pysp	*Pyrola* spp.	*Pyrola asarifolia* Michx. and *P. minor* L.
Rhin	*Rhodiolia integrifol.*	*Rhodiolia integrifolia* Raf.
	Rumex arcticus	*Rumex arcticus* Trautv.
SaLi	*Sagina Linnaei*	*Sagina Linnaei* Presl.
	Saxifraga tricuspid.	*Saxifraga tricuspidata* Rottb.
Setr	*Senecio triangularis*	*Senecio triangularis* Hook.
	Senecio yukonensis	*Senecio yukonensis* Porsild
Sesp	*Senecio* spp.	*Senecio* spp., including *S. lugens* Richards.

Somu	*Solidago multiradiata*	*Solidago multiradiata* Ait.
Stml	*Stellaria mon./long.*	*Stellaria monantha* Hult. or *S. longipes* Goldie
	Taraxacum sp.	*Taraxacum* sp.
	Valeriana capitata	*Valeriana capitata* Pall.
VeWo	*Veronica Wormskjoldii*	*Veronica Wormskjoldii* Roem. & Schult.
	Viola epipsila	*Viola epipsila* Ledeb.
spx1	forb sp.1	unknown broad-leafed forbs
	forb sp.2	
	forb sp.3	
graminoids		
Agsc	*Agrostis scabra*	*Agrostis scabra* Willd.
Casp	*Calamagrostis* spp.	*Calamagrostis canadensis* (Michx.) Beauv., *C. inexpansa* A. Gray and *C. lapponica* (Wahlenb.) Hartm.
Caaq	*Carex aquatilis*	*Carex aquatilis* Wahlenb.
	Carex aurea	*Carex aurea* Nutt.
Crsp	*Carex* spp.	*Carex brunnescens* Poir., *C. capillaris* L., *C. concinna* R. Br., *C. membranacea* Hook., *C. phaeocephala* Piper, *C. podocarpa* R. Br., *C. rupestris* All., *C. vaginata* Tausch
	Eriophorum sp.	*Eriophorum* sp.
grss	grass spp.	*Agropyron violaceum* (Hornem.) Lange, *Deschampsia caespitosa* (L.) Beauv. and *Festuca altaica* Trin.
Jusp	*Juncus* spp.	*Juncus biglumis* L. and *J. castaneus* Smith
Lupa	*Luzula parviflora*	*Luzula parviflora* (Ehrh.) Desv.
	Phleum alpinum	*Phleum alpinum* L.
	Poa spp.	*Poa alpigena* (Fr.) Lindm., *Poa alpina* L. and *Poa arctica* R. Br.
Trsp	*Trisetum spicatum*	*Trisetum spicatum* (L.) Richt.
lichens		
	Alectoria ochroleuca	*Alectoria ochroleuca* (Hoffm.) Mass.
	Cetraria com./hep.	*Cetraria commixta* (Nyl.) Th. Fr. or *C. hepatizon* (Ach.) Vain.
Cecu	*Cetraria cucullata*	*Cetraria cucullata* (Bell.) Ach.
	Cetraria ericetorum	*Cetraria ericetorum* Opiz.
Ceis	*Cetraria islandica*	*Cetraria islandica* (L.) Ach.
	Cetraria nigricans	*Cetraria nigricans* (Retz.) Nyl.

Cenv	*Cetraria nivalis*	*Cetraria nivalis* (L.) Ach.
Cepi	*Cetraria pinastri*	*Cetraria pinastri* (Scop.) S. Gray
	Cetraria richardsonii	*Cetraria richardsonii* (Hook.) Karnef.
	Cetraria sp.	*Cetraria* sp.
Clar	*Cladina arbuscula*	*Cladina arbuscula* (Wallr.) Rabenh.
	Cladina mitis	*Cladina mitis* (Sandst.) Hustich.
Clra	*Cladina rangiferina*	*Cladina rangiferina* (L.) Nyl.
Clst	*Cladina stellaris*	*Cladina stellaris* (Opiz) Brodo
Clam	*Cladonia amaurocraea*	*Cladonia amaurocraea* (Floerke) Schaer.
Clca	*Cladonia cariosa*	*Cladonia cariosa* (Ach.) Spreng.
Clce	*Cladonia cenotea*	*Cladonia cenotea* (Ach.) Schaer.
Ctce	*Cladonia cervicornal.*	*Cladonia cervicornalis* subsp. verticillata (Hoffm.) Schaer.
Clcb	*Cladonia cocc./bell.*	*Cladonia coccifera* (L.) Willd. or *C. bellidiflora* (Ach.) Schaer.
Clcr	*Cladonia crispata*	*Cladonia crispata* (Ach.) Flot.
Clma	*Cladonia macrophylla*	*Cladonia macrophylla* (Schaer.) Stenham.
	Cladonia pocillum	*Cladonia pocillum* (Ach.) O. Rich.
Clsu	*Cladonia sulphurina*	*Cladonia sulphurina* (Michx.) Fr.
Clun	*Cladonia uncialis*	*Cladonia uncialis* (L.) Wigg., may include *C. multiformis* Merr.
Clx1	*Cladonia* tapered	*Cladonia cornuta* (L.) Hoffm., *C. ecmocyna* Leight., *C. gracilis* (L.) Willd., *C. subulata* (L.) Wigg. and others with similar morphology
Clx2	*Cladonia* cup	*Cladonia chlorophaea* (Somm.) Spreng., *C. coniocraea* (Floerke) Spreng., *C. deformis* (L.) Hoffm., *C. fimbriata* (L.) Fr., *C. pleurota* (Floerke) Schaer., *C. pyxidata* (L.) Hoffm. and others with similar morphology
	Cladonia sp.3	unknown *Cladonia* sp.
Clx4	*Cladonia* sp.4	unknown *Cladonia* sp.
	Dactylina arctica	*Dactylina arctica* (Hook.) Nyl.
Near	*Nephroma arcticum*	*Nephroma arcticum* (L.) Torss.
Pape	*Pannaria pezizoides*	*Pannaria pezizoides* (G. Web.) Trev.
	Parmelia sp.	*Parmelia* sp.
Pahy	*Parmeliop. hyperopta*	*Parmeliopsis hyperopta* (Ach.) Arn.
Peap	*Peltigera aphthosa*	*Peltigera aphthosa* (L.) Willd.

Peca	*Peltigera canina*	*Peltigera canina* (L.) Willd.
	Peltigera malacea	*Peltigera malacea* (Ach.) Funck
Pepo	*Peltigera polydactyla*	*Peltigera polydactyla* (Neck.) Hoffm.
	Peltigera rufescens	*Peltigera rufescens* (Weiss.) Humb.
	Peltigera venosa	*Peltigera venosa* (L.) Hoffm.
	Peltigera sp.	*Peltigera* sp.
Pshy	*Psoroma hypnorum*	*Psoroma hypnorum* (Vahl) S. Gray
Socr	*Solorina crocea*	*Solorina crocea* (L.) Ach.
Stsp	*Stereocaulon* spp.	*Stereocaulon alpinum* Funck., *S. paschale* (L.) Hoffm., *S. rivulorum* Magn., *S. saxatile* Magn. and *S. tomentosum* Fr.
	Thamnolina sp.	*Thamnolina subuliformis* (Ehrh.) W. Culb. or *T. vermicularis* (Sw.) Ach. ex. Schaer.
	Umbilicaria spp.	*Umbilicaria cylindrica* (L.) Del. and *U. hyperborea* (Ach.) Hoffm.
crus	crustose	crustose and squamulose lichens (both saxicolous and terricolous)

bryophytes

Aupa	*Aulacomnium palustre*	*Aulacomnium palustre* (Hedw.) Schwaegr.
	Buxbaumia aphylla	*Buxbaumia aphylla* Hedw.
	Climacium dendroides	*Climacium dendroides* (Hedw.) Web. & Mohr
Disp	*Dicranum* spp.	*Dicranum* spp.
Drx1	*Drepanocladus* sp.1	*Drepanocladus* sp.
Drx2	*Drepanocladus* sp.2	*Drepanocladus aduncus* (Hedw.) Warnst. or *D. uncinatus* (Hedw.) warnst. or *Hypnum* sp.
Hysp	*Hylocomnium splendens*	*Hylocomnium splendens* (Hedw.) B. S. G.
	Leptobryum pyriforme	*Leptobryum pyriforme* (Hedw.) Wils.
Plsc	*Pleurozium schreberi*	*Pleurozium schreberi* (Brid.) Mitt.
Pocj	*Polytrichum com./jun.*	*Polytrichum commune* Hedw. and *P. juniperinum* Hedw.
Popi	*Polytrichum piliferum*	*Polytrichum piliferum* Hedw.
Post	*Polytrichum strictum*	*Polytrichum strictum* Brid.
Rhca	*Rhacomitrum canescens*	*Rhacomitrum canescens* (Hedw.) Brid.
Rhsp	*Rhizomnium* spp.	*Rhizomnium* spp. or other Mniaceae
Spsp	*Sphagnum* spp.	*Sphagnum* spp.

Toni	*Tomenthypnum nitens*	*Tomenthypnum nitens* (Hedw.) Loeske
pleu	pleurocarpic spp.	*other pleurocarpic mosses including: Brachythecium* sp., *Calliergon* sp., *Campylium stellatum* (Hedw.) C. Jens. and *Paludella squarrosa* (Hedw.) Brid.
acro	acrocarpic	acrocarpic mosses including: *Ceratodon purpureus* (Hedw.) Brid., *Pohlia nutans* (Hedw.) Lindb. and *Tortula ruralis* (Hedw.) Gaertn., Meyer, & Scherb.
live	liverwort	liverwort spp.
other plant species		
	Botrychium Lunaria	*Botrychium Lunaria* (L.) Sw.
Eqar	*Equisetum arvense*	*Equisetum arvense* L.
Eqsc	*Equisetum scirpoides*	*Equisetum scirpoides* Michx.
Eqsy	*Equisetum sylvaticum*	*Equisetum sylvaticum* L.
	Lycopodium alp./comp.	*Lycopodium alpinum* L. or *L. complanatum* L.
Lyac	*Lycopodium ann./clav.*	*Lycopodium annotinum* L. and *L. clavatum* L.
	Lycopodium Selago	*Lycopodium Selago* L.
alga	algae	algae

Appendix 6. Results of univariate nested analyses of variance for plant species composition among undisturbed areas, linear disturbance and borrow pits. Results are given for average cover and species richness per quadrat and per site of various taxonomic groups, as well as cover of shrub, litter, rock and bare ground. The first probability level measures the significance that the variation among disturbance types is greater than the variation among sites within each disturbance type. The second probability measures the significance that the variation among sites within disturbance types is greater than the variation among quadrats within sites. All categories are for percent cover except for number of species.

N = 690

DIST = disturbance type (borrow pits, linear disturbances, undisturbed)

SITE(DIST) = sites within each disturbance type (n=14,15,17 for borrow pits, linear disturbances and undisturbed sites respectively)

DF = degrees of freedom

P = probability

- = not significant at P<0.05

* = significant at P<0.05

** = significant at P<0.01

Total cover

MULTIPLE R: 0.846 SQUARED MULTIPLE R: 0.716

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	36.979	2	18.489	26.151	**
SITE(DIST)	30.419	43	0.707	17.073	**
ERROR	26.684	644	0.041		

Total number of species per quadrat

MULTIPLE R: 0.774 SQUARED MULTIPLE R: 0.599

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	5.626	2	2.813	13.023	**
SITE(DIST)	9.276	43	0.216	13.916	**
ERROR	9.983	644	0.016		

Total number of species per site

MULTIPLE R: 0.573 SQUARED MULTIPLE R: 0.329

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.230	2	0.115	9.730	**
ERROR	0.508	43	0.012		

Woody species

MULTIPLE R: 0.809 SQUARED MULTIPLE R: 0.654

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	136.056	2	68.028	42.920	**
SITE(DIST)	68.136	43	1.585	9.445	**
ERROR	108.040	644	0.168		

Number of woody species per quadrat

MULTIPLE R: 0.887 SQUARED MULTIPLE R: 0.787

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	38.177	2	19.089	49.072	**
SITE{DIST}	16.721	43	0.389	16.848	**
ERROR	14.864	644	0.023		

Number of woody species per site

MULTIPLE R: 0.360 SQUARED MULTIPLE R: 0.129

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.155	2	0.078	2.653	-
ERROR	1.256	43	0.029		

Betula glandulosa

MULTIPLE R: 0.696 SQUARED MULTIPLE R: 0.484

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	99.066	2	49.533	41.730	**
SITE{DIST}	51.034	43	1.187	4.782	**
ERROR	159.826	644	0.248		

***Salix* spp.**

MULTIPLE R: 0.773 SQUARED MULTIPLE R: 0.597

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	10.273	2	5.136	1.555	-
SITE{DIST}	142.007	43	3.302	20.715	**
ERROR	102.667	644	0.159		

Broad-leaved forbs

MULTIPLE R: 0.793 SQUARED MULTIPLE R: 0.629

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	15.240	2	7.620	3.479	*
SITE{DIST}	94.157	43	2.190	21.875	**
ERROR	64.465	644	0.100		

Number of broad-leaved forbs per quadrat

MULTIPLE R: 0.830 SQUARED MULTIPLE R: 0.689

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	6.687	2	3.343	3.782	*
SITE{DIST}	38.003	43	0.884	28.267	**
ERROR	20.135	644	0.031		

Number of broad-leaved forbs per site

MULTIPLE R: 0.460 SQUARED MULTIPLE R: 0.211

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	1.324	2	0.662	6.782	**
ERROR	4.196	43	0.098		

Graminoids

MULTIPLE R: 0.683 SQUARED MULTIPLE R: 0.466

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	3.781	2	1.891	2.587	-
SITE{DIST}	31.428	43	0.731	11.674	**
ERROR	40.319	644	0.063		

Number of graminoids per quadrat

MULTIPLE R: 0.731 SQUARED MULTIPLE R: 0.534

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	1.824	2	0.912	3.591	*
SITE{DIST}	10.909	43	0.254	14.694	**
ERROR	11.120	644	0.017		

Number of graminoids per site

MULTIPLE R: 0.722 SQUARED MULTIPLE R: 0.522

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	1.270	2	0.635	34.863	**
ERROR	0.783	43	0.018		

Lichens

MULTIPLE R: 0.733 SQUARED MULTIPLE R: 0.537

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	5.965	2	2.983	1.045	-
SITE{DIST}	122.723	43	2.854	16.589	**
ERROR	110.796	644	0.172		

Number of lichen species per quadrat

MULTIPLE R: 0.722 SQUARED MULTIPLE R: 0.521

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	1.079	2	0.539	0.984	-
SITE{DIST}	23.549	43	0.548	15.561	**
ERROR	22.666	644	0.035		

Number of lichen species per site

MULTIPLE R: 0.263 SQUARED MULTIPLE R: 0.069

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.103	2	0.051	1.359	-
ERROR	1.623	43	0.038		

***Cetraria* spp.**

MULTIPLE R: 0.727 SQUARED MULTIPLE R: 0.529

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	8.766	2	4.383	8.662	**
SITE{DIST}	21.771	43	0.506	12.004	**
ERROR	27.162	644	0.042		

***Cladina* spp.**

MULTIPLE R: 0.834 SQUARED MULTIPLE R: 0.695

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	68.185	2	34.092	12.520	**
SITE{DIST}	117.083	43	2.723	21.566	**
ERROR	81.311	644	0.126		

***Cladonia* spp.**

MULTIPLE R: 0.682 SQUARED MULTIPLE R: 0.465

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	3.144	2	1.572	1.387	-
SITE{DIST}	48.703	43	1.133	12.237	**
ERROR	59.607	644	0.093		

Peltigera spp.

MULTIPLE R: 0.467 SQUARED MULTIPLE R: 0.218

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	3.558	2	1.779	3.893	*
SITE{DIST}	19.671	43	0.457	3.533	**
ERROR	83.375	644	0.129		

***Stereocaulon* spp.**

MULTIPLE R: 0.739 SQUARED MULTIPLE R: 0.547

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	51.876	2	25.938	14.066	**
SITE{DIST}	79.306	43	1.844	10.922	**
ERROR	108.746	644	0.169		

Crustose lichens

MULTIPLE R: 0.622 SQUARED MULTIPLE R: 0.386

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	22.223	2	11.111	25.081	**
SITE{DIST}	19.050	43	0.443	4.353	**
ERROR	65.545	644	0.102		

Bryophytes

MULTIPLE R: 0.764 SQUARED MULTIPLE R: 0.584

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	62.506	2	31.253	16.921	**
SITE{DIST}	79.441	43	1.847	11.749	**
ERROR	101.267	644	0.157		

Number of bryophytes per quadrat

MULTIPLE R: 0.640 SQUARED MULTIPLE R: 0.410

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	3.905	2	1.952	11.689	**
SITE{DIST}	7.171	43	0.167	6.731	**
ERROR	15.956	644	0.025		

Number of bryophytes per site

MULTIPLE R: 0.582 SQUARED MULTIPLE R: 0.338

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.265	2	0.133	12.140	**
ERROR	0.470	43	0.011		

***Polytrichum* spp.**

MULTIPLE R: 0.682 SQUARED MULTIPLE R: 0.465

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	6.889	2	3.444	1.199	-
SITE{DIST}	123.538	43	2.873	12.311	**
ERROR	150.285	644	0.233		

Acrocarpic moss

MULTIPLE R: 0.542 SQUARED MULTIPLE R: 0.294

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	12.507	2	6.253	38.128	**
SITE{DIST}	7.054	43	0.164	2.246	**
ERROR	47.026	644	0.073		

Pleurocarpic moss

MULTIPLE R: 0.832 SQUARED MULTIPLE R: 0.693

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	122.205	2	61.102	15.838	**
SITE{DIST}	165.887	43	3.858	19.423	**
ERROR	127.913	644	0.199		

Other species (*Lycopodium* spp., *Equisetum* spp., algae)

MULTIPLE R: 0.712 SQUARED MULTIPLE R: 0.507

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	2.853	2	1.427	1.572	-
SITE{DIST}	39.044	43	0.908	14.380	**
ERROR	40.664	644	0.063		

Number of other species per quadrat

MULTIPLE R: 0.819 SQUARED MULTIPLE R: 0.671

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	1.803	2	0.902	2.361	-
SITE{DIST}	16.436	43	0.382	27.564	**
ERROR	8.930	644	0.014		

Number of other species per site

MULTIPLE R: 0.482 SQUARED MULTIPLE R: 0.233

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.644	2	0.322	6.341	**
ERROR	2.183	43	0.051		

***Equisetum* spp.**

MULTIPLE R: 0.813 SQUARED MULTIPLE R: 0.660

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	5.738	2	2.869	3.775	*
SITE{DIST}	32.659	43	0.760	24.771	**
ERROR	19.746	644	0.031		

***Lycopodium* spp.**

MULTIPLE R: 0.406 SQUARED MULTIPLE R: 0.165

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.581	2	0.291	4.343	*
SITE{DIST}	2.880	43	0.067	2.462	**
ERROR	17.520	644	0.027		

Shrub cover over 30 cm

MULTIPLE R: 0.715 SQUARED MULTIPLE R: 0.511

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	112.993	2	56.496	50.943	**
SITE{DIST}	47.693	43	1.109	4.651	**
ERROR	153.563	644	0.238		

Litter

MULTIPLE R: 0.771 SQUARED MULTIPLE R: 0.595

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	81.790	2	40.895	54.527	**
SITE{DIST}	32.230	43	0.750	6.215	**
ERROR	77.664	644	0.121		

Rock

MULTIPLE R: 0.877 SQUARED MULTIPLE R: 0.769

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	160.322	2	80.161	51.884	**
SITE{DIST}	66.419	43	1.545	14.644	**
ERROR	67.928	644	0.105		

Bare ground

MULTIPLE R: 0.716 SQUARED MULTIPLE R: 0.513

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	80.312	2	40.156	59.490	**
SITE{DIST}	29.045	43	0.675	4.191	**
ERROR	103.784	644	0.161		

Appendix 7. Results of univariate nested analyses of variance for plant species composition among linear disturbances. Results are given for average cover and species richness per quadrat and per site of various taxonomic groups, as well as cover of shrub, litter, rock and bare ground. The first probability level measures the significance that the variation among linear disturbance types is greater than the variation among sites within each linear disturbance type. The second probability measures the significance that the variation among sites within linear disturbance types is greater than the variation among quadrats within sites. All categories are for percent cover except for number of species.

N = 225

TRACK = linear disturbance type (access roads, bladed trails, multi-tracks, heavy-use tracks, bulldozer tracks)

SITE{TRACK} = sites within each linear disturbance type (n = 3, 3, 2, 2, 5; for access roads, bladed trails, multi-tracks, heavy-use track, bulldozer track sites respectively)

DF = degrees of freedom

P = probability

- = not significant at P<0.05

* = significant at P<0.05

** = significant at P<0.01

Total cover

MULTIPLE R: 0.540 SQUARED MULTIPLE R: 0.292

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.633	4	0.158	0.790	-
SITE{TRACK}	1.995	10	0.200	6.561	**
ERROR	6.387	210	0.030		

Total number of species per quadrat

MULTIPLE R: 0.522 SQUARED MULTIPLE R: 0.273

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.221	4	0.055	0.833	-
SITE{TRACK}	0.663	10	0.066	5.912	**
ERROR	2.355	210	0.011		

Total number of species per site

MULTIPLE R: 0.501 SQUARED MULTIPLE R: 0.251

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	229.517	4	57.379	0.837	-
ERROR	685.417	10	68.542		

Woody species

MULTIPLE R: 0.467 SQUARED MULTIPLE R: 0.218

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	2.766	4	0.692	0.770	-
SITE{TRACK}	8.993	10	0.899	4.479	**
ERROR	42.170	210	0.201		

Number of woody species per quadrat

MULTIPLE R: 0.537 SQUARED MULTIPLE R: 0.288

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.287	4	0.072	0.426	-
SITE{TRACK}	1.688	10	0.169	7.266	**
ERROR	4.879	210	0.023		

Number of woody species per site

MULTIPLE R: 0.430 SQUARED MULTIPLE R: 0.185

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	11.400	4	2.850	0.566	-
ERROR	50.333	10	5.033		

Betula glandulosa

MULTIPLE R: 0.383 SQUARED MULTIPLE R: 0.147

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	3.451	4	0.863	1.005	-
SITE{TRACK}	8.592	10	0.859	2.581	**
ERROR	69.911	210	0.333		

***Salix* spp.**

MULTIPLE R: 0.726 SQUARED MULTIPLE R: 0.528

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	24.800	4	6.200	2.484	-
SITE{TRACK}	24.957	10	2.496	11.768	**
ERROR	44.536	210	0.212		

Broad-leaved forbs

MULTIPLE R: 0.669 SQUARED MULTIPLE R: 0.448

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	14.497	4	3.624	3.316	-
SITE{TRACK}	10.930	10	1.093	7.333	**
ERROR	31.301	210	0.149		

Number of broad-leaved forbs per quadrat

MULTIPLE R: 0.684 SQUARED MULTIPLE R: 0.467

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	5.954	4	1.488	4.785	*
SITE{TRACK}	3.111	10	0.311	6.323	**
ERROR	10.332	210	0.049		

Number of broad-leaved forbs per site

MULTIPLE R: 0.364 SQUARED MULTIPLE R: 0.132

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	34.267	4	8.567	0.381	-
ERROR	224.667	10	22.467		

Graminoids

MULTIPLE R: 0.565 SQUARED MULTIPLE R: 0.319

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	3.411	4	0.853	1.921	-
SITE{TRACK}	4.444	10	0.444	5.559	**
ERROR	16.790	210	0.080		

Number of graminoids per quadrat

MULTIPLE R: 0.606 SQUARED MULTIPLE R: 0.367

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.683	4	0.171	1.082	-
SITE{TRACK}	1.582	10	0.158	8.503	**
ERROR	3.907	210	0.019		

Number of graminoids per site

MULTIPLE R: 0.485 SQUARED MULTIPLE R: 0.236

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	4.933	4	1.233	0.771	-
ERROR	16.000	10	1.600		

Lichens

MULTIPLE R: 0.709 SQUARED MULTIPLE R: 0.503

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	9.810	4	2.453	0.927	-
SITE{TRACK}	26.456	10	2.646	15.498	**
ERROR	35.848	210	0.171		

Number of lichen species per quadrat

MULTIPLE R: 0.727 SQUARED MULTIPLE R: 0.529

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	2.483	4	0.621	0.895	-
SITE{TRACK}	6.945	10	0.694	17.344	**
ERROR	8.408	210	0.040		

Number of lichen species per site

MULTIPLE R: 0.503 SQUARED MULTIPLE R: 0.253

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	138.083	4	34.521	0.848	-
ERROR	407.250	10	40.725		

***Cetraria* spp.**

MULTIPLE R: 0.585 SQUARED MULTIPLE R: 0.342

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	2.631	4	0.658	2.037	-
SITE{TRACK}	3.233	10	0.323	6.026	**
ERROR	11.266	210	0.054		

***Cladina* spp.**

MULTIPLE R: 0.704 SQUARED MULTIPLE R: 0.496

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	12.071	4	3.018	2.899	-
SITE{TRACK}	10.406	10	1.041	9.572	**
ERROR	22.831	210	0.109		

***Cladonia* spp.**

MULTIPLE R: 0.635 SQUARED MULTIPLE R: 0.403

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	3.125	4	0.781	0.932	-
SITE{TRACK}	8.384	10	0.838	10.335	**
ERROR	17.036	210	0.081		

***Peltigera* spp.**

MULTIPLE R: 0.404 SQUARED MULTIPLE R: 0.163

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	4.441	4	1.110	3.118	-
SITE{TRACK}	3.557	10	0.356	1.818	-
ERROR	41.091	210	0.196		

***Stereocaulon* spp.**

MULTIPLE R: 0.582 SQUARED MULTIPLE R: 0.339

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	11.872	4	2.968	3.396	-
SITE{TRACK}	8.743	10	0.874	4.566	**
ERROR	40.207	210	0.191		

Crustose lichens

MULTIPLE R: 0.453 SQUARED MULTIPLE R: 0.205

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.626	4	0.157	0.358	-
SITE{TRACK}	4.382	10	0.438	4.737	**
ERROR	19.426	210	0.093		

Bryophytes

MULTIPLE R: 0.522 SQUARED MULTIPLE R: 0.272

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	5.684	4	1.421	1.939	-
SITE{TRACK}	7.328	10	0.733	4.424	**
ERROR	34.785	210	0.166		

Number of bryophytes per quadrat

MULTIPLE R: 0.567 SQUARED MULTIPLE R: 0.321

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	1.081	4	0.270	2.195	-
SITE{TRACK}	1.234	10	0.123	5.292	**
ERROR	4.895	210	0.023		

Number of bryophytes per site

MULTIPLE R: 0.798 SQUARED MULTIPLE R: 0.637

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	26.567	4	6.642	4.379	*
ERROR	15.167	10	1.517		

***Polytrichum* spp.**

MULTIPLE R: 0.641 SQUARED MULTIPLE R: 0.411

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	16.324	4	4.081	1.994	-
SITE{TRACK}	20.475	10	2.047	8.169	**
ERROR	52.637	210	0.251		

Acrocarpic moss

MULTIPLE R: 0.401 SQUARED MULTIPLE R: 0.161

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.624	4	0.156	0.591	-
SITE{TRACK}	2.645	10	0.264	3.251	**
ERROR	17.086	210	0.081		

Pleurocarpic moss

MULTIPLE R: 0.731 SQUARED MULTIPLE R: 0.534

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	20.909	4	5.227	1.430	-
SITE{TRACK}	36.545	10	3.654	15.300	**
ERROR	50.158	210	0.239		

Other species (*Lycopodium* spp., *Equisetum* spp., algae)

MULTIPLE R: 0.563 SQUARED MULTIPLE R: 0.317

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	2.799	4	0.700	1.136	-
SITE{TRACK}	6.161	10	0.616	6.709	**
ERROR	19.285	210	0.092		

Number of other species per quadrat

MULTIPLE R: 0.719 SQUARED MULTIPLE R: 0.517

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	1.901	4	0.475	1.480	-
SITE{TRACK}	3.215	10	0.321	14.122	**
ERROR	4.781	210	0.023		

Number of other species per site

MULTIPLE R: 0.375 SQUARED MULTIPLE R: 0.141

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	3.000	4	0.750	0.409	-
ERROR	18.333	10	1.833		

***Equisetum* spp.**

MULTIPLE R: 0.713 SQUARED MULTIPLE R: 0.509

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	3.983	4	0.996	1.972	-
SITE{TRACK}	5.054	10	0.505	12.152	**
ERROR	8.734	210	0.042		

***Lycopodium* spp.**

MULTIPLE R: 0.411 SQUARED MULTIPLE R: 0.169

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	1.575	4	0.394	3.550	*
SITE{TRACK}	1.106	10	0.111	1.762	**
ERROR	13.181	210	0.063		

Shrub cover over 30 cm

MULTIPLE R: 0.461 SQUARED MULTIPLE R: 0.212

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	8.275	4	2.069	1.921	-
SITE{TRACK}	10.770	10	1.077	3.200	**
ERROR	70.678	210	0.337		

Litter

MULTIPLE R: 0.447 SQUARED MULTIPLE R: 0.200

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	4.036	4	1.009	2.257	-
SITE{TRACK}	4.470	10	0.447	2.762	**
ERROR	33.990	210	0.162		

Rock

MULTIPLE R: 0.453 SQUARED MULTIPLE R: 0.206

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	1.211	4	0.303	2.261	-
SITE{TRACK}	6.066	10	0.607	4.529	**
ERROR	28.126	210	0.134		

Bare ground

MULTIPLE R: 0.408 SQUARED MULTIPLE R: 0.166

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	1.878	4	0.470	0.655	-
SITE{TRACK}	7.178	10	0.718	3.319	**
ERROR	45.414	210	0.216		

Appendix 8. Results of the multivariate nested analyses of variance (MANOVA) for plant species composition among undisturbed areas, linear disturbances and borrow pits. Results are given for average cover and species richness of various taxonomic groups, as well as cover of shrub, litter, rock and bare ground. The first two tables are the multivariate tests of significance; these are separated since there were fewer samples for species richness per site. Following these tables are the results from the corresponding univariate F-tests with (2,43) degrees of freedom; these tests take into account the dependence on other variables in the MANOVA. The probability level measures the significance that the variation among disturbance types is greater than the variation among sites within each disturbance type. All categories are for percent cover except for the number of species.

DF = degrees of freedom
P = probability, significance of F

Multivariate test of significance for the average cover and average number of species per quadrat of all taxonomic groups listed below.

Test Name	Value	Approx. F	Hypoth. DF	Error DF	P
Pillais	1.37014	.98239	62.00	28.00	.538
Hotellings	16.41614	3.17732	62.00	24.00	.001
Wilks	.03420	1.84820	62.00	26.00	.043
Roys	.93998				

Multivariate test of significance for the average number of species per site of all major taxonomic groups.

Test Name	Value	Approx. F	Hypoth. DF	Error DF	P
Pillais	1.19531	8.06382	14.00	76.00	.000
Hotellings	5.79713	14.90691	14.00	72.00	.000
Wilks	.10320	11.16777	14.00	74.00	.000
Roys	.83989				

Univariate F-tests.

	F	P
Total cover	7.01427	.002
Total number of species per quadrat	4.82474	.013
Total number of species per site	9.73004	.000
Woody species	7.29029	.002
Number of woody species per quadrat	11.99834	.000
Number of woody species per site	2.65348	.082
Betula glandulosa	9.68575	.000
Salix spp.	.16601	.848
Broad-leaved forbs	.06601	.936
Number of forbs per quadrat	.10772	.898
Number of forbs per site	6.78245	.003
Graminoids	.29146	.749
Number of graminoids per quadrat	.52112	.598
Number of graminoids per site	34.86350	.000
Lichens	.36664	.695
Number of lichen species per quadrat	.89180	.417
Number of lichen species per site	1.35851	.268
Cetraria spp.	.77181	.468
Cladina spp.	1.67788	.199
Cladonia spp.	.78412	.463
Peltigera spp.	1.81079	.176
Stereocaulon spp.	.84166	.438
Crustose lichens	5.66128	.007
Bryophytes	2.63283	.083
Number of bryophytes per quadrat	1.12208	.335
Number of bryophytes per site	12.14038	.000
Polytrichum spp.	1.10183	.341
Acrocarpic moss	14.74340	.000
Pleurocarpic moss	4.22716	.021
Other species	.86822	.427
Number of other species per quadrat	.84894	.435
Number of other species per site	6.34053	.004
Equisetum spp.	1.18662	.315
Lycopodium spp.	.16169	.851
Shrub cover over 30 cm	7.35894	.002
Litter	5.76142	.006
Rock	15.44394	.000
Bare ground	0.03896	.000

Appendix 9. Results of the multivariate nested analyses of variance (MANOVA) for plant species composition among linear disturbance types. Results are given for average cover and species richness of various taxonomic groups, as well as cover of shrub, litter, rock and bare ground. The results are the univariate F-tests with (4,10) degrees of freedom; these tests take into account the dependence on other variables in the MANOVA. The probability level measures the significance that the variation among linear disturbance types is greater than the variation among sites within each linear disturbance type. Multivariate tests of significance were not available due to linear dependence of the variables. All categories are for percent cover except for the number of species.

P = probability, significance of F

	F	P
Total cover	1.31770	.328
Total number of species per quadrat	1.56868	.256
Woody species	1.30695	.332
Number of woody species per quadrat	.61238	.663
Betula glandulosa	1.14308	.391
Salix spp.	1.82435	.201
Broad-leaved forbs	1.83605	.199
Number of forbs per quadrat	2.13724	.150
Graminoids	1.15003	.388
Number of graminoids per quadrat	1.13814	.393
Lichens	1.38805	.306
Number of lichen species per quadrat	1.39278	.305
Cetraria spp.	1.54626	.262
Cladina spp.	2.36015	.123
Cladonia spp.	1.20256	.368
Peltigera spp.	2.00888	.169
Stereocaulon spp.	1.28903	.338
Crustose lichens	.09715	.981
Bryophytes	1.50280	.273
Number of bryophytes per quadrat	2.56965	.103
Polytrichum spp.	1.25655	.349
Acrocarpic moss	.18373	.942
Pleurocarpic moss	.96235	.469
Other species	.95242	.474
Number of other species per quadrat	1.32286	.327
Equisetum spp.	1.33528	.323
Lycopodium spp.	.68474	.619
Shrub cover over 30 cm	1.57564	.255
Litter	.32273	.856
Rock	.25751	.899
Bare ground	.96221	.469

Appendix 10. Matrices of pairwise comparison probabilities from Tukey multiple comparisons of data for which the variance among disturbance types was greater than the variance among sites within disturbance types (univariate nested ANOVA, Appendix 6). Probability values are given for differences between disturbance types: 1 = borrow pits, 2 = linear disturbances, 3 = undisturbed. Significant differences at $p<0.05$ are highlighted.

Total cover

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.001**	1.000

Total number of species per quadrat

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	0.083	1.000

Total number of species per site

	1	2	3
1	1.000		
2	**0.048**	1.000	
3	0.129	**0.000**	1.000

Woody species

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.037**	1.000

Number of woody species per quadrat

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.000**	1.000

Betula glandulosa

	1	2	3
1	**1.000**		
2	**0.000**	1.000	
3	**0.000**	**0.000**	1.000

Broad-leaved forbs

	1	2	3
1	1.000		
2	**0.001**	1.000	
3	**0.000**	**0.000**	1.000

Number of broad-leaved forbs per quadrat

	1	2	3
1	1.000		
2	**0.005**	1.000	
3	**0.000**	**0.000**	1.000

Number of broad-leaved forbs per site

	1	2	3
1	1.000		
2	0.575	1.000	
3	0.082	0.005	1.000

Number of graminoids per quadrat

	1	2	3
1	1.000		
2	0.000	1.000	
3	0.997	0.000	1.000

Number of graminoids per site

	1	2	3
1	1.000		
2	0.420	1.000	
3	0.000	0.000	1.000

***Cetraria* spp.**

	1	2	3
1	1.000		
2	0.003	1.000	
3	0.000	0.000	1.000

***Cladina* spp.**

	1	2	3
1	1.000		
2	0.000	1.000	
3	0.000	0.000	1.000

Peltigera spp.

	1	2	3
1	1.000		
2	0.007	1.000	
3	0.231	0.000	1.000

Stereocaulon spp.

	1	2	3
1	1.000		
2	0.000	1.000	
3	0.000	0.000	1.000

Crustose lichens

	1	2	3
1	1.000		
2	0.000	1.000	
3	0.000	0.095	1.000

Bryophytes

	1	2	3
1	1.000		
2	0.000	1.000	
3	0.000	0.553	1.000

Number of bryophytes per quadrat

	1	2	3
1	1.000		
2	0.000	1.000	
3	0.000	0.000	1.000

Number of bryophytes per site

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	0.099	**0.024**	1.000

Acrocarpic moss

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.000**	1.000

Pleurocarpic moss

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.009**	1.000

Number of other species per site

	1	2	3
1	1.000		
2	0.205	1.000	
3	0.196	**0.002**	1.000

***Equisetum* spp.**

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	0.427	1.000

***Lycopodium* spp.**

	1	2	3
1	1.000		
2	**0.013**	1.000	
3	0.364	**0.000**	1.000

Shrub cover over 30 cm

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.000**	1.000

Litter

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.007**	1.000

Rock

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.001**	1.000

Bare ground

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.000**	1.000

Appendix 11. Results of univariate nested analyses of variance for rooting zone depth, number of layers and soil characteristics in the mineral, tephra and organic layers, among undisturbed areas, linear disturbances and borrow pits. A separate analysis is performed for each soil characteristic in each layer. The first probability level measures the significance that the variation among disturbance types is greater than the variation among sites within each disturbance type. The second probability measures the significance that the variation among sites within disturbance types is greater than the variation among quadrats within sites.

DIST = disturbance type (borrow pits, linear disturbances, undisturbed)
SITE{DIST} = sites within each disturbance type
DF = degrees of freedom
P = probability
- = not significant at P<0.05
* = significant at P<0.05
** = significant at P<0.01

Rooting zone depth

N: 142 MULTIPLE R: 0.802 SQUARED MULTIPLE R: 0.644

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	2.274	2	1.137	6.695	**
SITE{DIST}	6.622	39	0.170	3.096	**
ERROR	4.442	81	0.055		

Number of layers

N: 142 MULTIPLE R: 0.797 SQUARED MULTIPLE R: 0.635

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.294	2	0.147	10.600	**
SITE{DIST}	0.540	39	0.014	2.275	**
ERROR	0.493	81	0.006		

pH in the mineral layer

N: 134 MULTIPLE R: 0.785 SQUARED MULTIPLE R: 0.616

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.752	2	0.376	3.547	*
SITE{DIST}	4.446	42	0.106	2.978	**
ERROR	3.164	89	0.036		

Gravel content in the mineral layer

N: 123 MULTIPLE R: 0.860 SQUARED MULTIPLE R: 0.739

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	1.535	2	0.768	2.058	-
SITE{DIST}	14.545	39	0.373	4.676	**
ERROR	6.461	81	0.080		

Water content in the mineral layer

N: 123 MULTIPLE R: 0.796 SQUARED MULTIPLE R: 0.634

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	1.272	2	0.636	9.638	**
SITE{DIST}	2.573	39	0.066	2.703	**
ERROR	1.978	81	0.024		

Organic matter content in the mineral layer

N: 123 MULTIPLE R: 0.779 SQUARED MULTIPLE R: 0.607

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	1.132	2	0.566	8.205	**
SITE{DIST}	2.691	39	0.069	2.880	**
ERROR	1.941	81	0.024		

Hygroscopic water content in the mineral layer

N: 123 MULTIPLE R: 0.796 SQUARED MULTIPLE R: 0.633

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.468	2	0.234	8.232	**
SITE{DIST}	1.109	39	0.028	3.007	**
ERROR	0.766	81	0.009		

Clay content in the mineral layer

N: 47 MULTIPLE R: 0.987 SQUARED MULTIPLE R: 0.975

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.460	2	0.230	4.428	*
SITE{DIST}	2.024	39	0.052	92.927	**
ERROR	0.045	81	0.001		

Silt content in the mineral layer

N: 47 MULTIPLE R: 0.992 SQUARED MULTIPLE R: 0.984

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.347	2	0.174	6.245	**
SITE{DIST}	1.084	39	0.028	304.601	**
ERROR	0.007	81	0.000		

Sand content in the mineral layer

N: 47 MULTIPLE R: 0.994 SQUARED MULTIPLE R: 0.989

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.827	2	0.414	6.037	**
SITE{DIST}	2.672	39	0.069	84.292	**
ERROR	0.066	81	0.001		

Width of the tephra layer

N: 23 MULTIPLE R: 0.723 SQUARED MULTIPLE R: 0.522

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.180	2	0.090	0.774	-
SITE{DIST}	1.508	13	0.116	0.791	-
ERROR	1.468	10	0.147		

pH in the tephra layer

N: 26 MULTIPLE R: 0.938 SQUARED MULTIPLE R: 0.880

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.000	2	0.000	0.183	-
SITE{DIST}	0.007	13	0.001	5.383	**
ERROR	0.001	10	0.000		

Gravel content in the tephra layer

N: 26 MULTIPLE R: 0.894 SQUARED MULTIPLE R: 0.800

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.003	2	0.002	0.009	-
SITE{DIST}	2.500	13	0.192	2.535	-
ERROR	0.759	10	0.076		

Water content in the tephra layer

N: 26 MULTIPLE R: 0.918 SQUARED MULTIPLE R: 0.844

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.077	2	0.038	0.946	-
SITE{DIST}	0.526	13	0.040	4.667	**
ERROR	0.087	10	0.009		

Organic matter content in the tephra layer

N: 26 MULTIPLE R: 0.997 SQUARED MULTIPLE R: 0.994

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.054	2	0.027	0.511	-
SITE{DIST}	0.689	13	0.053	17.119	**
ERROR	0.031	10	0.003		

Hygroscopic water content in the tephra layer

N: 26 MULTIPLE R: 0.838 SQUARED MULTIPLE R: 0.702

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.001	2	0.000	0.085	-
SITE{DIST}	0.056	13	0.004	1.654	-
ERROR	0.026	10	0.003		

Width of the organic layer

N: 28 MULTIPLE R: 0.775 SQUARED MULTIPLE R: 0.601

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.013	1	0.013	0.130	-
SITE{DIST}	1.089	11	0.099	3.300	-
ERROR	0.450	15	0.030		

pH in the organic layer

N: 28 MULTIPLE R: 0.778 SQUARED MULTIPLE R: 0.606

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.003	1	0.003	7.396	*
SITE{DIST}	0.004	11	0.000	1.056	-
ERROR	0.005	15	0.000		

Gravel content in the organic layer

N: 28 MULTIPLE R: 0.636 SQUARED MULTIPLE R: 0.405

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.091	1	0.091	0.339	-
SITE{DIST}	2.960	11	0.269	0.948	-
ERROR	4.258	15	0.284		

Water content in the organic layer

N: 28 MULTIPLE R: 0.687 SQUARED MULTIPLE R: 0.472

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.036	1	0.036	0.491	-
SITE{DIST}	0.803	11	0.073	1.443	-
ERROR	0.758	15	0.051		

Organic matter content in the organic layer

N: 28 MULTIPLE R: 0.609 SQUARED MULTIPLE R: 0.371

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.000	1	0.000	0.009	-
SITE{DIST}	0.392	11	0.036	0.809	-
ERROR	0.660	15	0.044		

Hygroscopic water content in the organic layer

N: 28 MULTIPLE R: 0.715 SQUARED MULTIPLE R: 0.511

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DIST	0.021	1	0.021	0.610	-
SITE{DIST}	0.381	11	0.035	1.546	-
ERROR	0.336	15	0.022		

Appendix 12. Results of univariate nested analyses of variance for rooting zone depth, number of layers and soil characteristics in the mineral layer in linear disturbances. A separate analysis is performed for each soil characteristic in each layer. The first probability level measures the significance that the variation among linear disturbance types is greater than the variation among sites within each linear disturbance type. The second probability measures the significance that the variation among sites within linear disturbance types is greater than the variation among quadrats within sites.

TRACK = linear disturbance type (access roads, bladed trails, multi-tracks, heavy-use tracks, bulldozer tracks)

SITE{TRACK} = sites within each linear disturbance type

DF = degrees of freedom

P = probability

- = not significant at P<0.05
- * = significant at P<0.05
- ** = significant at P<0.01

Rooting zone

N: 50 MULTIPLE R: 0.748 SQUARED MULTIPLE R: 0.559

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.650	4	0.162	0.819	-
SITE{TRACK}	1.784	9	0.198	2.405	*
ERROR	2.720	33	0.082		

pH in the mineral layer

N: 48 MULTIPLE R: 0.693 SQUARED MULTIPLE R: 0.480

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.002	4	0.001	0.949	-
SITE{TRACK}	0.005	9	0.001	2.259	*
ERROR	0.008	33	0.000		

Gravel content in the mineral layer

N: 47 MULTIPLE R: 0.766 SQUARED MULTIPLE R: 0.587

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	2.625	4	0.656	1.563	-
SITE{TRACK}	3.780	9	0.420	3.908	**
ERROR	3.547	33	0.107		

Water content in the mineral layer

N: 47 MULTIPLE R: 0.703 SQUARED MULTIPLE R: 0.495

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.378	4	0.095	1.114	-
SITE{TRACK}	0.764	9	0.085	2.823	**
ERROR	0.993	33	0.030		

Organic matter content in the mineral layer

N: 47 MULTIPLE R: 0.664 SQUARED MULTIPLE R: 0.441

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.132	4	0.033	0.340	-
SITE{TRACK}	0.875	9	0.097	2.488	*
ERROR	1.289	33	0.039		

Hygroscopic water content in the mineral layer

N: 47 MULTIPLE R: 0.660 SQUARED MULTIPLE R: 0.436

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.057	4	0.014	0.356	-
SITE{TRACK}	0.359	9	0.040	2.583	*
ERROR	0.510	33	0.015		

Clay content in the mineral layer

N: 18 MULTIPLE R: 0.904 SQUARED MULTIPLE R: 0.818

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.045	4	0.011	1.112	-
SITE{TRACK}	0.091	9	0.010	14.373	**
ERROR	0.023	33	0.001		

Silt content in the mineral layer

N: 18 MULTIPLE R: 0.962 SQUARED MULTIPLE R: 0.925

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.142	4	0.036	4.605	*
SITE{TRACK}	0.069	9	0.008	35.486	**
ERROR	0.007	33	0.000		

Sand content in the mineral layer

N: 18 MULTIPLE R: 0.954 SQUARED MULTIPLE R: 0.910

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
TRACK	0.440	4	0.110	3.852	*
SITE{TRACK}	0.257	9	0.029	17.928	**
ERROR	0.053	33	0.002		

Appendix 13. Results of the multivariate nested analysis of variance (MANOVA) for rooting zone depth, number of layers and soil characteristics in the mineral, tephra and organic layers, among undisturbed areas, linear disturbances and borrow pits. The first two tables are the separate multivariate tests of significance for each layer. Following these tables are the results from the corresponding univariate F-tests with (2,39), (2,13) and (1,10) degrees of freedom for the mineral, tephra and organic layers. These tests take into account the dependence on other variables in the MANOVA. The probability level measures the significance that the variation among disturbance types is greater than the variation among sites within each disturbance type.

DF = degrees of freedom
P = probability, significance of F

Multivariate test of significance for soil characteristics of mineral layer

Test Name	Value	Approx. F	Hypoth. DF	Error DF	P
Pillais	.27512	.49446	20.00	62.00	.959
Hotellings	.34850	.50532	20.00	58.00	.954
Wilks	.73446	.50056	20.00	60.00	.956
Roys	.23421				

Multivariate test of significance for soil characteristics of tephra layer

Test Name	Value	Approx. F	Hypoth. DF	Error DF	P
Pillais	.32347	.28941	12.00	18.00	.983
Hotellings	.45600	.26600	12.00	14.00	.986
Wilks	.68263	.28046	12.00	16.00	.984
Roys	.30338				

Multivariate test of significance for soil characteristics of organic layer

Test Name	Value	Approx. F	Hypoth. DF	Error DF	P
Pillais	.45746	84319	6.00	6.00	.579
Hotellings	.84319	.84319	6.00	6.00	.579
Wilks	.54254	.84319	6.00	6.00	.579
Roys	.45746				

Univariate F-tests.

	F	P
Rooting zone depth	.24179	.786
Number of layers	2.23634	.120
mineral layer		
pH	.85974	.431
Gravel content	.11667	.890
Water content	.67227	.516
Organic matter content	.28433	.754
Hygroscopic water content	.96124	.391
Clay content	1.03171	.366
Silt content	2.86019	.069
Sand content	1.19852	.313
tephra layer		
Width	.01419	.986
pH	1.66340	.227
Gravel content	.04308	.958
Water content	.08339	.920
Organic matter content	.23340	.795
Hygroscopic water content	1.07977	.368
organic layer		
Width	.91642	.359
pH	.10659	.750
Gravel content	2.54654	.139
Water content	.79348	.392
Organic matter content	.23695	.636
Hygroscopic water content	.45449	.514

Appendix 14. Results of the multivariate nested analysis of variance (MANOVA) for rooting zone depth, number of layers and soil characteristics in the mineral layer in linear disturbances. The multivariate test of significance is followed by are the results from the corresponding univariate F-tests with (4,9) degrees of freedom. These tests take into account the dependence on other variables in the MANOVA. The probability level measures the significance that the variation among linear disturbance types is greater than the variation among sites within each linear disturbance type.

DF = degrees of freedom
P = probability, significance of F

Multivariate test of significance for soil characteristics of mineral layer

Test Name	Value	Approx. F	Hypoth. DF	Error DF	P
Pillais	2.68991	.91255	36.00	16.00	.606
Wilks	.00137	.73243	36.00	5.48	.742
Roys	.96010				

Univariate F-tests.

	F	P
Rooting zone depth	.73116	.593
pH	1.12232	.404
Gravel content	.06638	.990
Water content	.63035	.653
Organic matter content	.43961	.777
Hygroscopic water content	.44007	.777
Clay content	.61347	.664
Silt content	3.08411	.074
Sand content	.93345	.487

Appendix 15. Matrices of pairwise comparison probabilities from Tukey multiple comparisons of data for which the variance of soil characteristics among disturbance types was greater than the variance among sites within disturbance types (univariate nested ANOVA, Appendix 11). Probability values are given for differences between disturbance types: 1 = borrow pits, 2 = linear disturbances, 3 = undisturbed. Significant differences at $p<0.05$ are highlighted.

Rooting zone depth

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	0.480	1.000

Number of layers

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.000**	**0.014**	1.000

pH in the mineral layer

	1	2	3
1	1.000		
2	**0.001**	1.000	
3	**0.000**	0.996	1.000

Water content in the mineral layer

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.004**	0.609	1.000

Organic matter content in the mineral layer

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.006**	0.275	1.000

Hygroscopic water content in the mineral layer

	1	2	3
1	1.000		
2	**0.000**	1.000	
3	**0.002**	0.406	1.000

Clay content in the mineral layer

	1	2	3
1	1.000		
2	**0.005**	1.000	
3	0.056	0.117	1.000

Silt content in the mineral layer

	1	2	3
1	1.000		
2	**0.001**	1.000	
3	**0.012**	**0.036**	1.000

Sand content in the mineral layer

	1	2	3
1	1.000		
2	0.001	1.000	
3	0.006	0.018	1.000

pH in the organic layer

	1	2
1	1.000	
2	0.013	1.000